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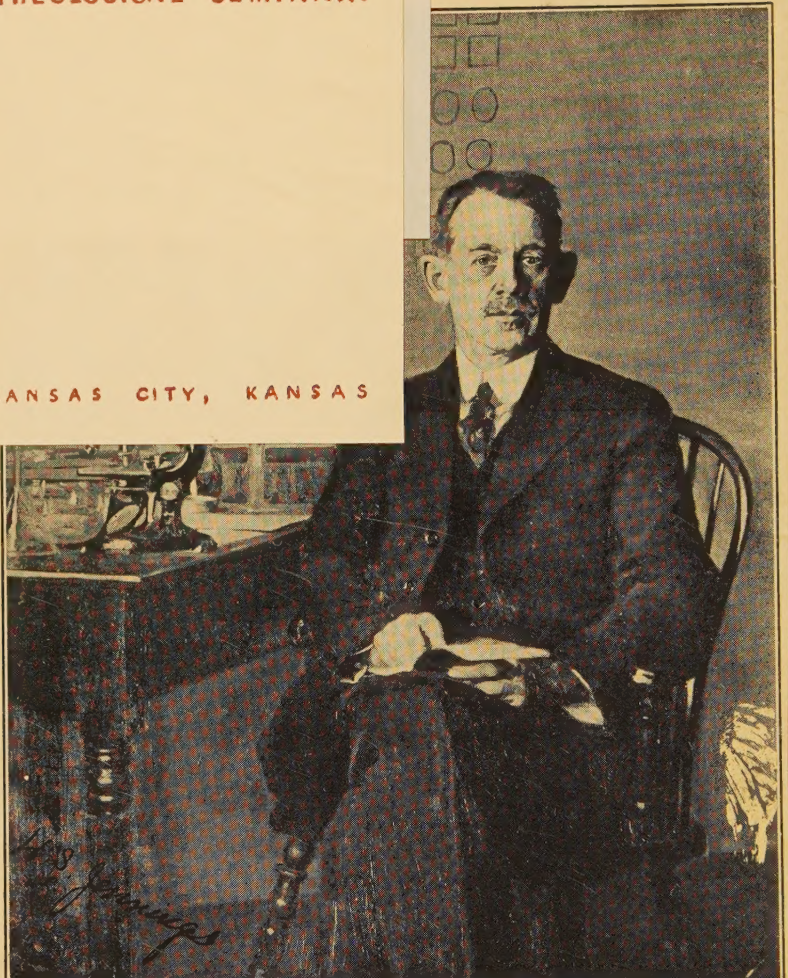
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THE BIOLOGICAL BASIS
OF HUMAN NATURE

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OF HUMAN NATURE

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TO CALVIN B. BRIDGES

to whose profound and constructive investigations all students of Genetics are deeply indebted

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PREFACE

This volume is an attempt to present those aspects of modern experimental biology that are of most interest in considering the problem of human personality and society. It deals with the origin, development and nature of the traits which distinguish individuals, and which in man make up character; and with some of the relations of these matters to social questions. The material is drawn mainly from the relatively new sciences of Genetics and Experimental Embryology. An effort is made to present it in non-technical language, though for a few important things unknown to common speech the technical terms are the only ones available.

The first five chapters summarize the biological foundations for the matters dealt with later. They are necessarily more technical than the others; they are compelled to present certain points that have not yet become familiar, but which in time will be a part of the every-day knowledge of all educated persons. Understanding of the more general questions dealt with in later chapters depends absolutely on a grasp of the matters presented in these chapters.

Chapters six to eight deal with the relations of this fundamental knowledge to certain more problematical questions of life and mind, chapter eight presenting certain historical aspects of these matters. Chapters nine to twelve inclusive take up the application of this knowledge to some social problems. Chapter thirteen stands by itself; it is speculative. The three final chapters are devoted to aspects of the problem of evolutionary change.

References to sources, and other comments, are gathered into notes at the end of each chapter. They are designed merely as keys by which the reader may follow further any subjects which interest him. The books or papers referred to will usually be found to contain titles of other works along the same line, through which the entire field of knowledge may be explored.

For permission to make use of material previously published in the form of articles or addresses, the author is indebted to the *Forum, Plain Talk, Science,* and the *Survey-Graphic.* He is indebted for important aid in the preparation of the volume to Louise B. Jennings, Ruth Stocking Lynch, and Harold Heath.

Baltimore, January 4, 1930.

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INTRODUCTION

What has biology to say that is of interest to men, not as zoologists or botanists, but as human beings? What has biology to contribute to the understanding of our lives and of the world in which we live?

Human beings are samples of the things with which biology deals. They appear as individuals, and the rest of the material of biology appears also, in the main, as individuals. The greatest questions of biology deal with the origin and nature of individuals, their characteristics, their likenesses and their differences. The diversity among living individuals is the most striking fact about them, the fact of most practical importance; and it is the matter on which biology has most to say. Human individuals are diverse—in their appearance, and in their behavior. And each has a separate consciousness, a separate identity; so that the inward experience of any one of them is a distinct thing from that of all others. In some or all of these respects they are typical of the material of biology.

How does it happen that individuals are thus diverse, both outwardly and inwardly? Why has my neighbor tastes and opinions so different from my own? Why does he conduct himself in a manner that may seem to me undesirable; a manner so diverse from that which I would practice under the same conditions? Why is one man fitted for one sort of work, another for another sort; and some for none at all? Why do precise experiments in the laboratory of psychology give with different individuals diverse and inconstant results? Why are my own children so diverse from me and from each other? What is it that makes the behavior of human beings so incalculable, inconsistent, astonishing? These are the most practical questions of life; and the most interesting in theory.

On these questions biology has much to say. It has worked out a systematic science of the differences between individuals; a science far from complete, but illuminating so far as it goes. There are two main classes of differences between individuals. 1. On the one hand, individuals are in many ways diverse at the very beginning of their separate existence, when they are single cells; these diversities come directly from their parents. Many of the later differences between developed individuals are due to these original differences. Knowledge of the original diversities, of how they are produced, of their nature and consequences, has advanced far. It constitutes what is called the study of heredity, or more properly, the science of Genetics.

On the other hand, as everyone knows, individuals may become changed by the experiences that they pass through; by 2. the conditions under which they live and develop. This therefore is another source of differences between individuals. An individual that has developed at a high temperature may be diverse in some respects from one that has developed at a low temperature. A person that has learned something is diverse from one that has not; a person that has undergone a great emotional shock is diverse from one that has not.

By the interplay of the differences existing at the beginning of life with those that arise through later experience are brought about all the infinitely numerous kinds of diversities that we find among the individuals we meet in the world. By the interaction of the diverse individuals so produced, with each other and with their organic and inorganic environments, arise societies and civilizations. By the changes in the inborn characteristics as generations pass, together with the changes in the outer environment, arise the transformations of organisms in succeeding ages; arises the process of evolution. To understand individuality, to understand human nature and animal nature and vegetable nature, to understand society and civilization, the two classes of diversities must be examined separately, then in their interaction and consequences; and in their changes with the passage of time. This is the task of the present volume.

THE BIOLOGICAL BASIS
OF HUMAN NATURE

I

THE ORIGINAL DIFFERENCES BETWEEN INDIVIDUALS; AND THEIR CONSEQUENCES

In higher organisms, including man, the individual originally exists as two separate minute pieces, which come from two pre-existing individuals that we call the parents. Its life as a single individual begins with the union of these two pieces into one cell. The fact that we are each formed from parts of two diverse individuals has extraordinary and momentous consequences.

In its earliest condition the new individual is a single cell with a single nucleus (figure 1), it is the fertilized egg. This cell, as everyone knows, divides repeatedly, producing many cells; producing ultimately the entire body, composed of millions of cells.

The Genes

Observation and experiment have shown that the original cell contains a great number of distinct and separable substances, existing as minute particles. The development of an individual is brought about by the interaction of these thousand substances—their interaction with each other, with other parts of the cell, and with material taken from outside. It is known that different individuals start with diverse sets of these substances, and that the way a given individual develops, what he becomes, what characteristics he gets, what peculiarities he shows, depend, other things being equal, on what set of these substances he starts with. Different individuals are made as it were on diverse recipes; and the diverse recipes give different results. Much is known of the results of altering only a single one of the thousand different substances present in the original cell, and of altering several or many. Some combinations of them give imperfect individuals, feebleminded, deformed, monstrous. Others give normal individuals, others superior individuals. There are combinations giving every intermediate type, some yielding slightly imperfect individuals, lazy, stupid or silly; and there are combinations that produce genius. No two individuals, in such an organism as man, are concocted on the same recipe (save in the rare cases known as identical twins). It is clearly proved experimentally that the diverse combinations yield structural and physiological differences of all types and grades, including diversities in behavior, in what we call mentality.

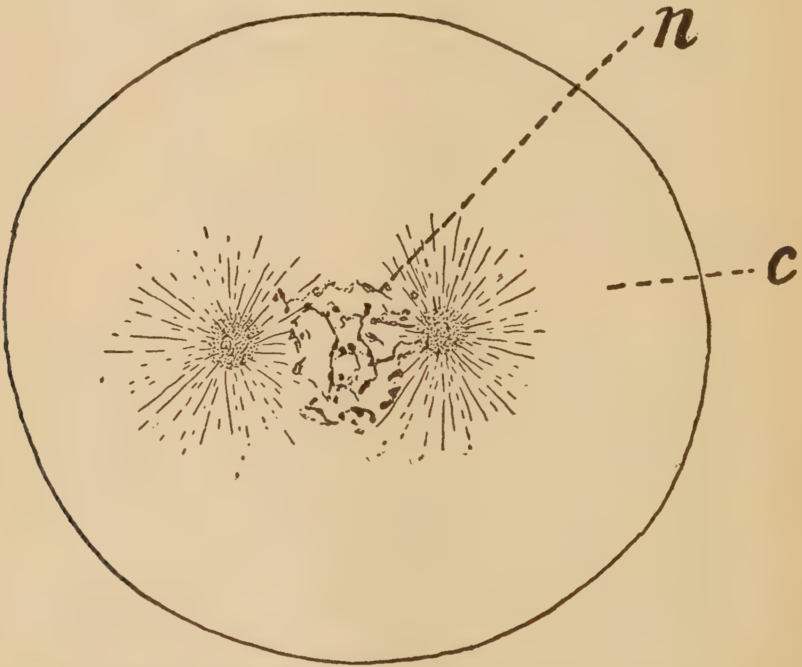


Figure 1—Individual in the earliest stage, the fertilized egg of the starfish. c, cytoplasm; n, nucleus, showing the small dark chromosomes. Based on the photograph in Wilson's Atlas of Fertilization, Plate VI, figure 24. (Columbia University Press, 1895.)

These many diverse substances present at the beginning of development are called the *genes*. The genes exist in the two pieces that unite to form the new individual. They were present in the two parents from which the two pieces came; so that the genes are transmitted to us directly from our parents.

The genes exist in the egg cell as a great number of extremely minute particles, which are grouped together to form structures that are visible under the microscope, and are known as *chromosomes* (figures 3 and 4). The chromosomes, with their included genes, constitute a vesicle in the interior of the cell, known as the *nucleus*. The egg cell consists of a mass of jelly-like material, known as *cytoplasm,* in which is imbedded the nucleus, with its chromosomes and genes (figure 1).

The Genetic System

Many of the most important features of development and of individuality result from the way the genes are disposed in the cells, their actual physical arrangement and consequent behavior. The way diverse individuals develop, the peculiarities that they show, the so-called laws of heredity, the extraordinary resemblances and differences between parents and offspring—all these things depend largely on the arrangement and behavior of the genes. The genes in their arrangement and operation constitute a system comparable in importance to the nervous or digestive systems; we may call them the *Genetic System*. To understand heredity and its results we must have in mind a picture of the genetic system and its method of operation. To try to grasp these matters without such a picture is a hopeless task. As well may one attempt to understand the movements and reactions of organisms without a knowledge of their nervous and muscular systems; or to understand digestion, knowing nothing of the digestive organs and their action. Anyone who declines the labor of becoming familiar with the fundamental features of the genetic system and its method of operation cuts himself off from the possibility of understanding the nature of man and the origin

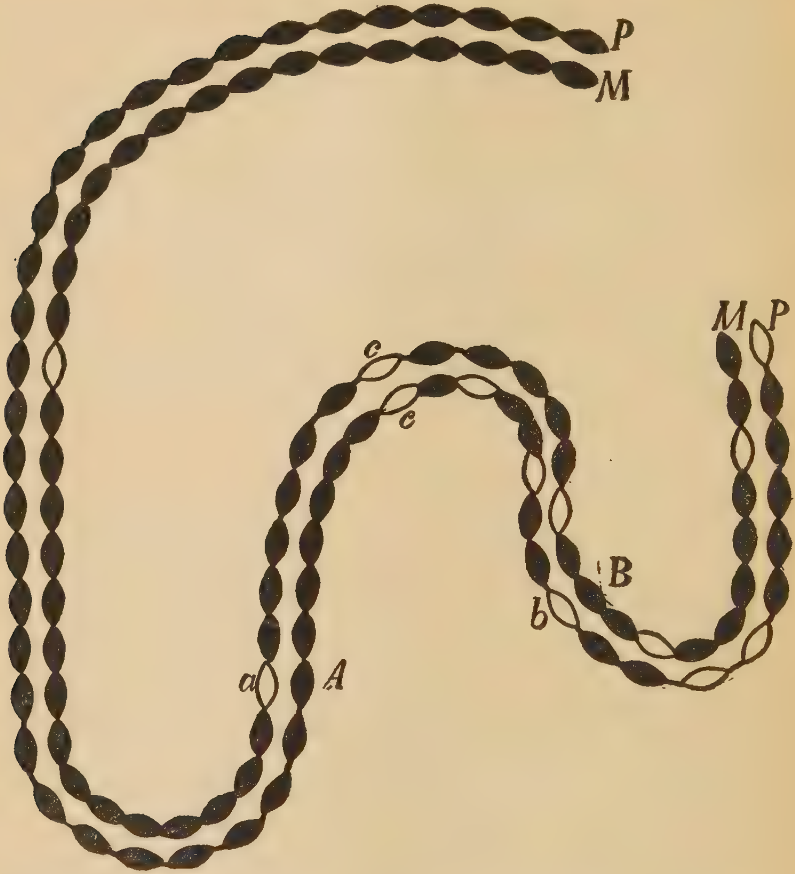


Figure 2—Diagram to illustrate the arrangement and action of the genes in the genetic system. The genes, represented by the spindle-shaped bodies, arranged in consecutive order, in long paired strings, the chromosomes. One string (P) of the pair comes from the father, the other (M) from the mother. Thus the genes themselves are in pairs, one member of each pair from the father, one from the mother. The genes shown in white are to be conceived as defective genes.

of his peculiarities. To a presentation of that system and its action we therefore turn. A knowledge of many details is essential; here as nowhere else great results follow from small causes.

The genes are present in the nucleus of the cell with which the individual starts (and in all the cells produced from it). In the nuclei it is known that they are strung up in long strings, like strings of a thousand beads (see figures 2, 5, 6, 7, etc.). These strings are what are called the chromosomes. The separate chromosomes are pieces into which the total string of beads is divided; separate segments of it, each containing many genes. At certain periods in the life of the cell the strings of genes are unfolded and widely drawn out; then it is that minute particles arranged in consecutive linear order like beads are visible under the microscope (figure 3). It appears probable that these particles (known as *chromomeres*) show the position of the genes, if they are not to be looked on as themselves the genes. They show just the paired consecutive

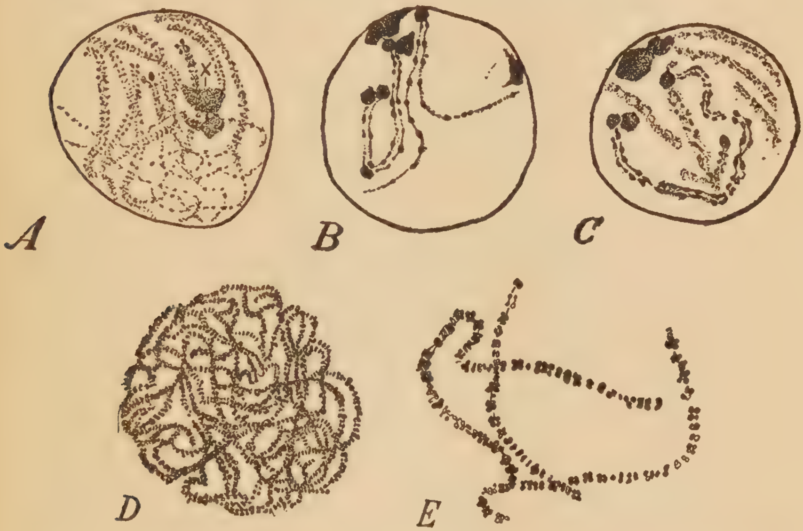


Figure 3—Structure of chromosomes as seen under the microscope, showing the minute paired particles (chromomeres) of which they are composed. A, B, C, chromomeres in the chromosomes of the grasshopper, after Wenrich (1916). D, E, chromomeres in the chromosomes of the lily, after Belling (1928). E shows a portion of D at a higher magnification. The chromomeres probably show the position of the genes.

arrangement known to be that in which the genes occur. At other periods the strings of genes are coiled or folded into bundles; it is these that are seen as thick chromosomes of various forms (figure 4). For an understanding of the behavior and effects of the genes, they must be pictured in linear order, as shown in the diagram of figure 2.

It is known that each of the thousand genes is a distinctive substance, having a definite function, a particular work to do in producing the new individual; so that if any one of them is destroyed or changed, development is altered in a definite way, and the resulting individual shows a corresponding change in his characteristics: a change perhaps in the color of his eyes, the shape of his nose, his stature; or in his temper or temperament.

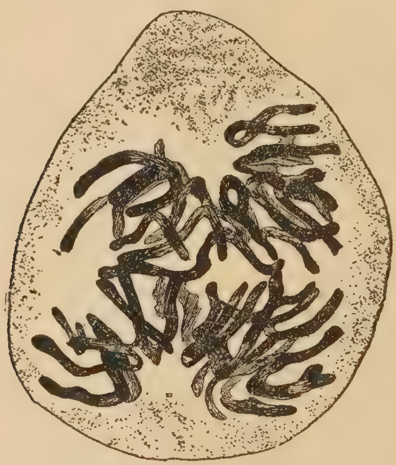


Figure 4—Chromosomes in the condensed condition, in a dividing cell of the salamander, Amblystoma.

It is known that each different kind of a gene has its regular and invariable place in the string. Thus the different genes can be named or numbered, and a particular one, as number 4 or number 47, is always the same gene, with the same role to play, and found at the same place in the chromosomes.

A further matter is known concerning the genes and their arrangement—a matter of extreme practical importance—a matter that is the key to many of the puzzles and problems and paradoxes of humanity, and of biology in general. This is the fact that each of our parents gives us a complete set of genes, strung up in the way we have described. So we have in every cell two such strings of genes, each one complete in itself, as represented in the diagram of figure 2. We are therefore double with respect to our genes. Each of the two sets in a cell contains all the materials that are necessary for producing an individual; a fact that has strange consequences. The mother gives us all the materials required for producing an individual of a certain type; the father also gives us the materials for producing another individual of another type. So we start life as double individuals. We are each in a sense two individuals, two diverse persons—rather thoroughly blended; but in certain respects not completely blended. This doubleness has a very great effect on life.

The doubleness applies to each of the thousand diverse substances or genes with which we begin life. Each kind is present in every cell in two doses, forming a pair of genes. One gene from each pair is from the father, one from the mother. The order and arrangement of the genes is then that shown in figure 2: a set of pairs arranged in longitudinal strings. In some animals, particularly certain insects, the two paired strings seemingly remain side by side during life, as indicated in the diagram. In others the two diverge at times, but become paired again at certain critical periods. For understanding the action of the genes, for understanding heredity, for understanding the nature of man, a picture of this paired arrangement (figure 2) must be kept in mind; it is the key to many of the riddles of biology.

The different pairs of genes have different functions in development. The two members of any one pair of genes (as A and a, figure 2) have the same general function. If one of the two has to do with producing the color of the eyes, so has its mate. If one has to do with building up some part of the brain, so has the other. If one influences the growth of the body, so does the other. But now a fact of extreme practical importance! Though the two members of a particular pair of genes have the same kind of work to do, they usually differ in the way they do that work. The one from the father may tend to produce a certain eye color, that from the mother to produce a different eye color. One from the father may tend to produce a poor brain and so a stupid individual; its mate from the mother may tend to produce a good brain, and so an intelligent individual. One of a pair may do its work well, another ill. One of the two genes of a pair (from father or mother) may be deficient or defective in some way. If its work is to lay down pigment in hair, skin and eyes, it may fail to do this properly, yielding what is called an albino, with white hair and skin and pink eyes. The other gene, from the other parent, may however perform the function fully, so that owing to its presence pigment is properly laid down. A certain gene may fail in laying a proper foundation for the brain; the result will be to produce a feeble-minded individual—unless there is also present, as its mate, a gene that performs fully this function. There are gene defects or deficiencies of every possible degree and kind, from slight differences in acuteness of senses, or in industry or patience, up to such serious defects as result in feeble-mindedness or insanity. It is rare, in organisms reproducing from two parents, for father and mother to give to any of the pairs genes exactly alike in their action. In any individual, therefore, many or most of the pairs will have the two genes somewhat diverse. Gene defects, or at least inequalities, slight or serious, are very common; so that every human being bears a few or many of them.

The advantages of having two parents, the advantages of being double, are therefore obvious. A gene from the father may be defective; if this were the only gene for that function, the child would be correspondingly defective: would be perhaps an albino, or stupid, or feebleminded. But the corresponding gene (of the same pair) from the mother may be normal. Then as a rule this normal gene performs the entire function, so that the child is normal: is not an albino, not stupid, not feebleminded (as the case may be). Thus the defectiveness of one gene of a pair has as a rule no evil consequences, or so little as to be scarcely perceptible. The doubleness of the genes therefore acts as an insurance; the individual has two chances instead of one to get each function in development properly performed. Only if both genes of a given pair are defective—that from the father and that from the mother—does the required function fail (as a rule), so that only in such a case is the individual produced defective—without pigment, stupid, lazy, feebleminded, or the like (compare figure 2, at cc).

It appears that this insurance through doubling of the genes is the chief biological ground for our having two parents instead of one. Gene defects are so common that without this doubling—the two genes of each pair coming each from a different source—defective individuals would be far commoner than they are. Organisms reproducing from two parents have a great advantage in this respect over those reproducing from a single parent. This may be the ground for the fact that most organisms reproduce at times, if not invariably, from two parents; although many of the lower organisms reproduce for long periods from a single parent.

When one gene of a pair is defective and the other is not, and the latter then produces normal development, the characteristic produced by the normal gene is called dominant, while the characteristic that tends to be produced by the defective gene is called recessive. So albinism, or lack of pigment, is recessive; it appears in the individual only if both of the genes required for producing the pigment are defective (as at cc, figure 2). The normal condition, with pigment in hair, skin and eyes, is dominant; it appears in the individual even if one of the required genes is defective, provided the other is not (as at A, figure 2). The dominant condition, of course, is manifested more frequently than the recessive one, if the normal and recessive genes are equally numerous; this is why it is advantageous that there should be two genes to each pair. It turns out, as is well known, that when dominant and recessive genes are equally numerous, and there is random mating among the individuals, those that show the dominant peculiarity are three times as numerous as those that show the recessive peculiarity.

While it is the general rule that defective conditions are recessive, so that dominance and recessiveness correspond on the average to advantageous and disadvantageous, or to better and worse, there are exceptions to this. There are many recessive characteristics that give no indication of being disadvantageous. So the lighter colors of the eye in man are recessive with respect to the darker colors. That is, if one gene of a pair is of the sort that yields blue eyes, the other of the sort that yields brown eyes, the latter gene produces it effect, and the individual has brown eyes. Here the gene that carries the development farthest—that lays down more pigment—is the one whose effect appears. But there is no known disadvantage in a blue eye, as compared with a brown one. The indications are that in general when the two members of a pair of genes are diverse, it is the one that carries the developmental function farthest that prevails in its effects, giving an individual that shows the characteristics which it produces. As defective conditions are very generally the result of not carrying out developmental processes fully, most defects are recessive.

Yet a considerable number of seriously defective conditions are known that are dominant, or partly dominant. In these cases the gene yielding the defect produces its results, in full or in part, even when a normal gene is present in the same pair. Such is the case with certain defects and deformities in man; for example, the conditions known as *brachydactyly,* in which the fingers are short, having but two joints in place of three. Union of two or more fingers side by side is likewise a dominant defect. A considerable number of dominant defects are known in that classic type in our knowledge of heredity, the fruit-fly; one of these (bar-eye) is shown in figure 20. In many or most of these cases the presence of a normal gene in the same pair with the defective one considerably reduces the ill effects of the defective gene, so that the characteristic manifested is an intermediate one. It appears possible that such dominant or partially dominant injurious genes carry the development beyond the normal condition, in an abnormal direction. This is not certain, however, and it is not always clear why one gene should be dominant rather than its mate.

But dominant harmful characteristics are so rare, as shown by the very fully studied case of the fruit-fly (Drosophila), that it is on the average nearest correct to think of defective characteristics as in the main recessive; recessive characteristics as in the main defective ones—inferior on the whole to the dominant condition.

How the Genetic System Works in Heredity

Observe how the system just described works out in the relation of the child's characteristics to those of his parents or other relatives. The dependence of the child's characteristics on the genes that he receives from his parents is what is called heredity. Each parent, we know, gives one of the two genes from each of his pairs to each child, so that the child possesses the same number of pairs of genes as did the parents.

A given individual may then be personally normal, but may nevertheless carry about with him defective genes. He may himself be patient, industrious, intelligent, but he may have concealed within himself, as it were, another personality, submerged, "recessive"; a personality that is irritable, lazy, stupid. That is, he may carry imperfect genes, that taken alone would yield an irritable, lazy or stupid person. And these are the genes that some of his children will get. What we get from our parents may give us the same characteristics that our parents possess. But we may also get from our parents something that they have been carrying about unknown to themselves and to others; something that gives us characteristics very diverse from the ones our parents show. The fact that we are double with respect to our genes makes heredity give many surprising results. It may give the result that "like produces like"; but it may also give the result that parents produce offspring very unlike themselves.

Examine how these things work in some of the commonest cases. Suppose that a certain defective gene tends to produce laziness or stupidity or feeblemindedness. A parent has two such defective genes in one of his pairs(figure 5, P), so that he is personally lazy or stupid or feebleminded. But the other parent has both genes of that pair normal (figure 5, M) ; this parent does not show these undesirable qualities. Each parent gives one gene of that pair to the offspring. So the child gets in that pair one normal gene, one defective one (figure 5, F). The normal gene performs the required function properly, so that the child is not lazy, or stupid, or feebleminded (as the case may be), although it has one of the defective genes. We may say that the child "takes after" one of his parents, not the other; takes after the superior parent, in this case. Such results may follow for all sorts of characteristics: for features, stature, eye color, or the like, as well as for characteristics that express themselves mainly in behavior.

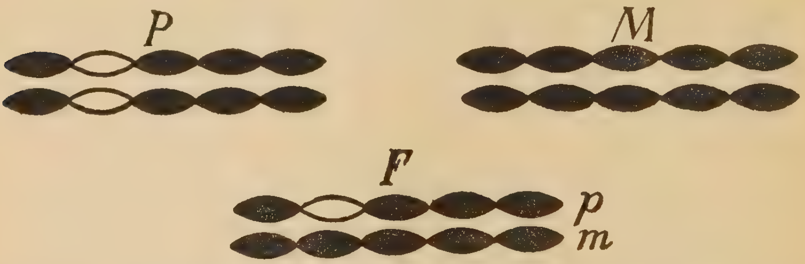


Figure 5—Diagram of a portion (five pairs) of the chains of genes in two parents, P, and M, and in one of their offspring F, to illustrate the workings of heredity. The father (P) has two defective genes (white) in one of his pairs (the second) and is therefore personally defective. The mother (M) has both genes normal in this second pair. The child receives one of the sets of genes from the father (*p*), one from the mother (*m*). It therefore has in all its pairs at least one normal gene and so is not personally defective.

Or the child may "take after" the inferior parent. Suppose that, as before, one parent has two defective genes in a certain pair and so is himself defective, while the other has but one and is therefore not defective (figure 6). When each gives a member of this pair to the offspring, some of the latter will get a defective gene from both parents (figure 6, F, *a*). Such children will then show the defect; will be in this respect like the defective parent. Others among the children will get only one defective gene in that pair (figure 6, F, *b*). Such children will be like the superior parent.

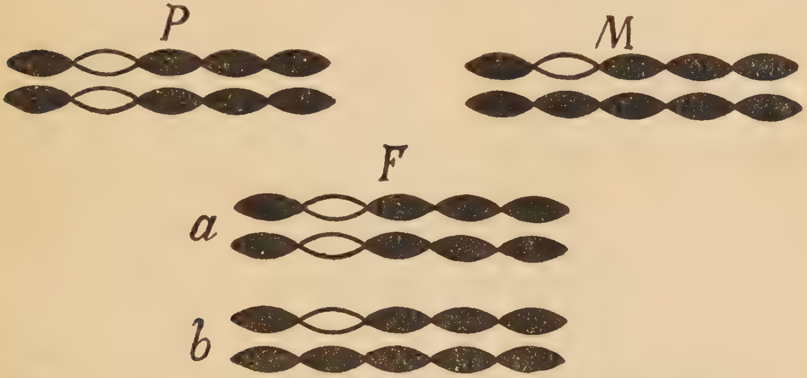


Figure 6—Diagram of the results in heredity in cases where one parent (P) has two defective genes (white) in a certain pair, the other parent (M) one defective gene in that pair. Some of the children (F) receive two defective genes in that pair (*a*) and are therefore personally defective; others only one (*b*), so that such are not personally defective.

But often the child does not "take after" either of his parents; he shows characteristics that do not appear in either parent. He may be inferior to both parents, showing defects that neither of them possesses. Or he may be superior to both parents, having the defects of neither. How does this happen?

Suppose that both parents are normal in themselves, but each has in the same particular pair one defective gene (figure 7). Then some of the children will get a defective gene from both parents (figure 7, F, *a*). A child with such a gene may then be lazy or stupid or feebleminded, or otherwise defective, though neither parent showed this characteristic. And this is not because he has not been properly brought up, nor because he has had poor nutrition, nor because he had a harmful shock before he was eighteen months old (though these things may do great harm if they occur); nor because of anything else (in such cases) save the fact that he received a bad combination in one of his gene-pairs—two defective genes, one from each parent.

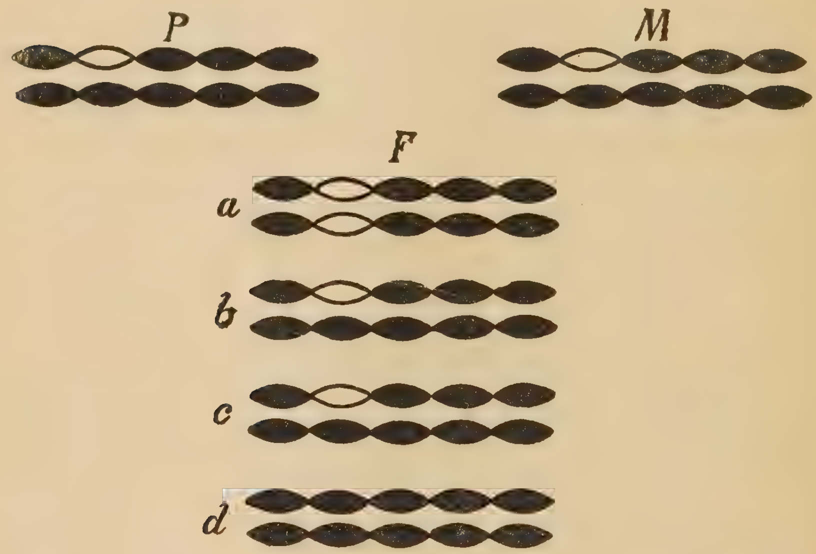


Figure 7—Diagram of genes, to illustrate the results in heredity when each parent has one defective gene (white) in the same pair. The parents, P and M, having a normal gene in each pair, are not defective. Of the children (F), some receive a defective gene from each parent, as at *a*; such will be personally defective. Others receive but one defective gene (*b* and *c*), or none (*d*); these will not be defective.

Some of the children of these same parents (three-fourths of them, on the average) will not get two defective genes in this pair, but only one or none (figure 7, *b, c, d*). Such children will lack the defects; they will be very different from the children that have the two defective genes. This sort of thing occurs with great frequency both with respect to very slight defects or inequalities of all sorts, and with respect to serious defects.

It occurs also with respect to dominant and recessive characteristics that are essentially indifferent in their effects on the individual, as in the case of eye colors. It is one of the chief reasons why the different children of a family are in various respects unlike each other, and unlike their parents.

But the children will sometimes be not only unlike the parents, but superior to them. This is an extremely important matter, playing a very great role in the reproduction of all organisms, including man. It is essential to see just how it occurs, if we are to understand the biological problems of society, of populations, either in man or other organisms. Two parents may both be seriously defective, perhaps in the same characteristic, and yet produce offspring that are all without the personal defects. In this way two parents that are both lazy or stupid may produce offspring that are industrious and of lively intelligence; even two parents that are feebleminded may produce normal children. This is because the faults of the two parents are due to defects in diverse pairs of genes. The genes of two such parents are represented in figure 8, at P and M. The parent P is defective in both genes of the second gene-pair; the parent M is defective in both genes of the fourth pair. In reproduction one gene from each of the pairs

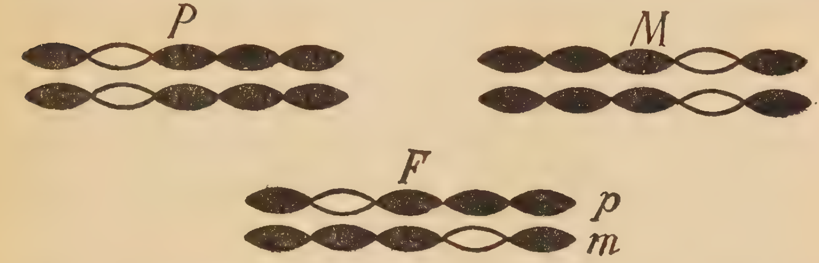


Figure 8—Diagram of genes in parents and offspring, to show how inferior parents may produce superior offspring. The father (P) has both genes defective (white) in the second pair shown; the mother (M) both defective in the fourth pair; both are therefore personally defective. The offspring (F), receiving one set of genes (*p* and *m*) from each parent, has no pair in which both genes are defective (white); it is therefore not personally defective. Each parent supplies a normal gene for the pair that is defective in the other parent.

is taken from each parent, and put with the corresponding gene from the other parent to form the gene-pairs of the offspring. And now, as figure 8 shows, in the child (F) none of the pairs has two defective genes. The mother supplies a normal gene for the father's defective (second) pair, the father supplies a normal gene for the mother's defective (fourth) pair. The children are therefore quite without the defects which were manifest in the two parents. One parent may have been stupid, the other lazy; the children are bright and industrious. The happy results are not due, in such a case, to the children's having better advantages than the parents, better education or better living conditions (though these things may also make a great difference). They are due to the contribution by the two parents of genes that supplement each other, so that each supplies what was lacking in the other. The children "take after" neither of the parents, in respect to these defects.

Even if the two parents manifest defects in the same characteristics, often the defects are due to different gene-pairs in the two cases, so that the children will not have the defect. As set forth above, even two feebleminded parents might in such a case produce offspring that are not feebleminded. This is one of the most important matters in heredity, and one generally neglected. Anyone who wishes to understand the origin of the characteristics of human individuals, or those of other organisms, should have a clear idea of the situation that gives rise to these results.

The essential point is that in the development of any individual all the thousand genes interact, work together, like a lot of chemicals in a physician's prescription. To produce even any single feature or characteristic, this interaction must take place. It is not correct, as was at one time generally supposed to be the case, that each particular characteristic is represented by one single gene (see Chapter VIII). On the contrary, to produce even so simple a characteristic as the color of the eye, many genes must interact. In the fruit-fly, the organism whose heredity is best known, it is found that at least fifty pairs of genes coöperate to produce the usual red color of the eye. Some lay a foundation on which the eye is built up; till this foundation is laid no color can appear. Others, after the eye has been formed, lay a basis for the color itself; others have specific functions in producing the proper chemicals for the pigment. If then any one of these genes is altered, is defective, the eye and its color are not properly compounded; the eye color will not appear, or will be imperfect, or diverse from the usual condition. By changing any one of the fifty genes of the fruit-fly that take part in producing the eye color, the color is altered; eyes of other color are produced; or there is no pigment in the eye; or it is structurally imperfect. The same situation is found for all characteristics, in the fruit-fly or in ourselves. Any feature or characteristic, structural, physiological or mental, can be changed or made defective by altering any one of the many different genes that coöperate to produce it. It is known that feeblemindedness may result from a defect in one pair of genes; such a pair must play some important part in laying a foundation for the brain. But in some individuals this will be one particular pair, in some another, out of the great number of gene-pairs required to build up a normal brain.

Personal peculiarities that are identical or closely similar may be produced by defects or alterations in diverse pairs of genes. In the fruit-fly the relative positions of many of the genes in the chromosomes have been determined, so that they can be represented on maps, and designated by the use of a system comparable to that giving the latitude or longitude of a place on the globe (figure 31). Alteration of a gene at the point 52.5 in the second chromosome causes the eye to be of a purplish color instead of red. Alteration of another gene at the point 43 in the third chromosome yields likewise a purplish color; and the same is true of alteration of another gene at the point 44.4 in the first chromosome. These three genes, each yielding purplish eyes, have received diverse names; the first is called "purple," the second "maroon," the third "garnet." When two purple-eyed parents are mated, in which the purple color is due to alteration of the same gene in the two, the children all have the purple eyes (see the diagram, figure 9). But when two purple-eyed parents are mated in which the purple color is due to alteration of different genes in the two cases (figure 8), the children have perfect normal red eyes. Each of the two defective parents contributes what is lacking in the other parent, so that the children are not defective. Many other cases of this sort are known. It is commonly said that two parents recessive for the same characteristic produce only children that are like themselves in being recessive for that characteristic. But this is true only if the recessive characteristics of the two parents are due to the same pair of genes, as in figure 9. If on the other hand they are due to diverse gene-pairs, then the offspring are not like the parents, but show the dominant or perfect condition of this characteristic. And it is very common that defects in the same characteristics of the two parents are due to the defectiveness of different gene-pairs; so that their offspring are all normal. So in the fruit-fly, individuals with small "vestigial" wings (figure 10, A) may be mated with others that have no wings (figure 10, B); the offspring will have no wing defects whatever, but all have normally formed wings (figure 10, C). Again, individuals without pigment in the eyes ("white eyes") may be crossed with others that have no eyes at all ("eyeless"); the offspring have perfect eyes. This method of action is one of the commonest in heredity.

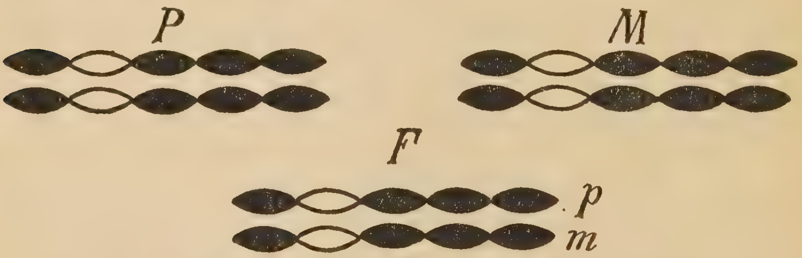


Figure 9—Diagram of genes, to illustrate the results in heredity when two defective parents, P and M, have both genes defective (white) in the same pair. The offspring F then receive one defective gene in that pair from each parent; such offspring are therefore personally defective, like the parents.

So in man, two parents might be both seriously defective, might both be stupid or lazy or feebleminded, but as a result

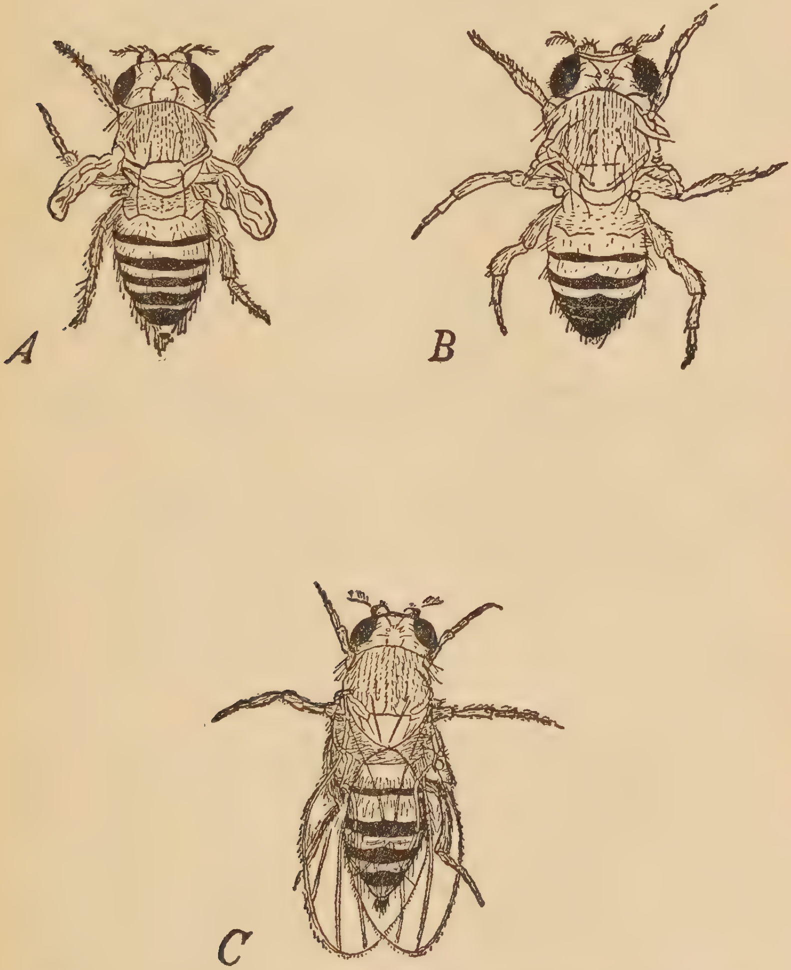


Figure 10—Mating of two defective parents, yielding normal offspring. A, parent with vestigial wings; B, parent with no wings. Such parents mated would yield normal offspring having no wing defects (C), because the defects of the two parents are due to defective genes in different pairs, as illustrated in figure 8. The figures are taken from separate figures in the Genetics of Drosophila, by Morgan, Bridges and Sturtevant.

of defects in different pairs of genes, as in the diagram of figure 8. One member of each gene-pair is taken from each parent and these are placed together to form the offspring. The mother supplies again a normal gene for the father's defective pair; the father a normal gene for the mother's defective pair. The children (figure 8, F) are therefore quite without the parental defect, although it was manifest in both parents.

This supplying of supplementary genes by the two parents may occur for many defective pairs in the same mating. A mother may have half a dozen serious personal defects, resulting from defective genes in a number of different gene-pairs; and the same may be true of the father. But if their gene defects are in different pairs in the two cases, the children will have one normal gene for each of the defective pairs (figure 11). They will therefore have none of the numerous defects shown by the parents; they will be far superior to their parents. Thus parents both of whom are slow, foolish, lacking industry and ambition, may produce children that have none of these defects, but are quick, intelligent, industrious, ambitious, so forming what we call superior individuals. This is in large

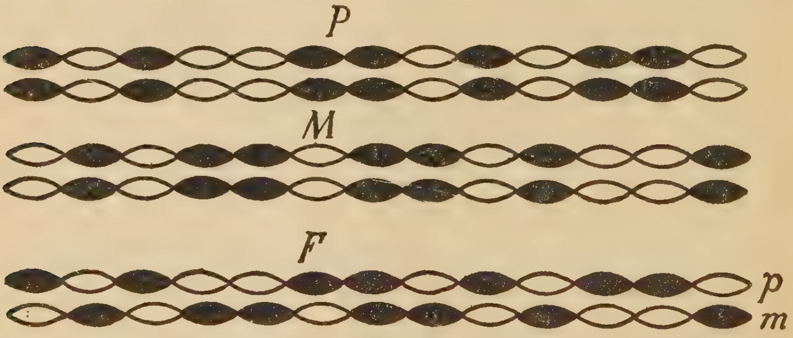


Figure 11—Diagram illustrating how parents showing many heredity defects may produce offspring with none. The father (P) has many pairs of genes with both members defective (white), and the same is true of the mother (M). But their defects are in different pairs; hence the offspring (F) receive in every pair at least one normal gene (black), and are therefore without the parental defects.

measure the origin of superiority, of genius, in man. It is the result of an unusual combination of genes, due to the contribution of a number of supplementary genes by the two parents.

This method of action plays a large role in the organisms in which heredity has been studied fully. In the fruit-fly, hundreds of types of defective individuals are known, resulting from recessive defects in the hundreds of well-explored diverse genes. When any two of these defective individuals are mated, the progeny are normal, except in cases where the defects of the two parents lie in the same gene-pair. In domesticated plants and animals the results of combining supplementary genes from the two parents is often most striking. Two diverse races of maize, both short, weak, spindling, and producing almost no yield of corn, when mated together give large, vigorous offspring, with a high yield of corn. Some authorities are of the opinion that in these cases the supplying of supplementary genes is not the only cause of the increased vigor of the offspring, but that the crossing of diverse races has in some other way a tendency to increase the vigor of the offspring.[1] But there can be no doubt that much, if not all, of the improvement in the offspring over their parents is due to supplementary genes from the two parents. For this action is readily demonstrated when individuals with known diverse recessive characteristics are mated.

When parents are closely related, the gene defects of the two are likely to lie in the same pairs. For they have gotten part of their genes from the same ancestors, and some of these common genes are likely to have been defective. In unrelated parents, on the other hand, the gene defects have arisen independently, in different ancestors, and are therefore not likely to lie in the same pairs. This is the reason why unrelated parents, and particularly those belonging to different racial groups, or coming from different parts of the country, frequently give superior offspring. Their children do not get the same gene defects in both members of their gene-pairs; hence the defective genes have little or no effect.

All this has its obverse side. By the production of new combinations in which the genes of the parents supplement each other, superior individuals are produced. By the taking apart of these combinations and the making of new ones in which the genes are not supplementary, inferior individuals are produced. The method of recombinations may work to produce defectives as well as normals, fools or knaves as well as geniuses. A large number of genes that are defective in greater or less degree are scattered about through the species; often producing no detectable effects, because protected by normal genes in the same pair. When there is mating between two normal individuals that each have certain defective genes in the same pairs (figure 12), then to some of their offspring each will contribute a defective gene of the same pair. The result is the production of defective individuals, inferior individuals, weak-eyed, susceptible to tuberculosis, stupid, lazy, or otherwise defective. From two superior parents may thus be produced offspring that are defective in several or many diverse respects, as is illustrated in the diagram of figure 12. To this method of action is due the origin of many of the hereditarily defective individuals, the persons we consider inferior.

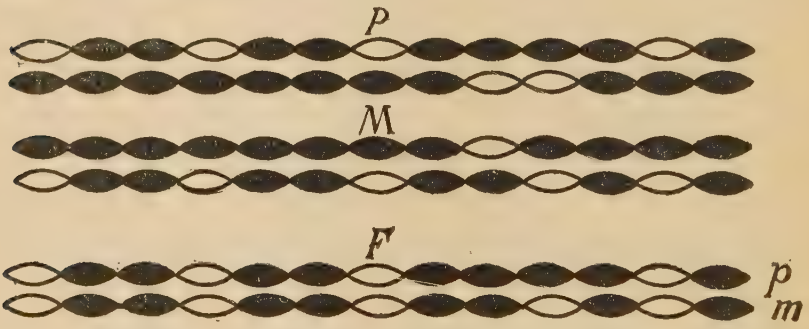


Figure 12—Diagram showing how parents (P and M) having no personal defects may produce offspring (F) with many personal defects. Each parent has a single defective gene (white) in several of his pairs; and these defective genes are in the same pairs in each parent. In consequence, some (not all) of the offspring may receive two defective genes in many pairs, as shown at F; such will show many personal defects.

Thus the production of individuals of exceptional type, both superior and inferior, is in the main the result of the production of new combinations of genes in the mating of two diverse parents. Superior individuals are produced when the two parents contribute supplementary genes to the different gene-pairs, so that in the offspring all poor or defective genes are accompanied, in the same pair, each by a gene of high type. Inferior individuals are produced when each parent contributes a poor or defective gene to the same gene-pair, so that the children have many pairs with both genes defective. Most individuals in such a species as man are intermediate; they have some poor genes that are unprotected by better ones in the same pair; others that are properly protected.

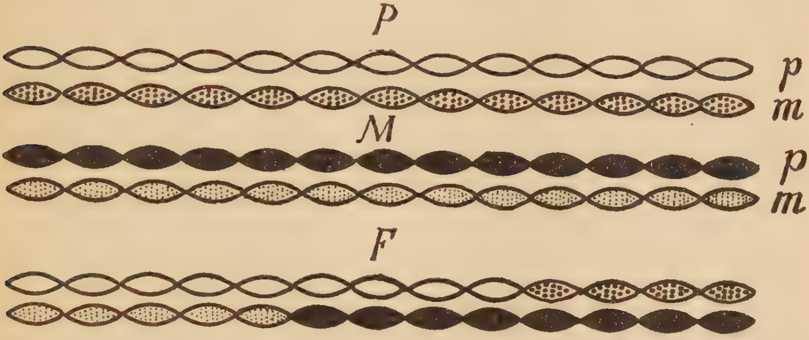


Figure 13—Diagram to illustrate recombination of grandparental genes in the offspring (F). The father (P) has one chain of genes (p) derived from the paternal grandfather, the other (m) from the paternal grandmother. The mother (M) similarly has one chain from each of the maternal grandparents (p and m). In the child (F), a recombination of part of the genes from the four grandparents is found, as indicated by the different types of shading.

Another method of forming new combinations of genes is in operation as the generations pass; a method less direct than that already described, but of equal importance in its effects. Any individual, as P or M in figure 13, gets two sets or strings of genes, one from his father, one from his mother. When two such individuals (P and M) mate to produce the next generation, each now contributes one of his strings of genes to each child. It may be his maternal string, in which case the child will have many of the same genes that his grandmother possessed, and will tend to be like his grandmother in many characteristics. Or the parent may contribute his paternal string, in which case the child will have a tendency to resemble his grandfather. But in most cases a recombination of paternal and maternal strings will have taken place within the parent. Half of the maternal string may unite with half of the paternal string; or three-quarters of the maternal with one-quarter of the paternal, as illustrated in figure 13, at F. The recombinations may occur in any proportions. Now the child of P and M will get from each parent, not simply the maternal string or the paternal string, but a string combined from the two. That is, he will get now from each parent a new combination of genes, partly from the grandmother and partly from the grandfather. This kind of recombination is greatly facilitated, and even made practically inevitable, by the fact that the string of genes borne by any individual is separated into a number of segments, which we call the different chromosomes (figure 4). The parent P will then give some maternal segments to his offspring, some paternal segments; and similiarly for the parent M.

Thus the child gets in this way a new combination of the genes that were derived originally from his four grandparents. One of his grandparents may have been dull and slow, but industrious and ambitious; on account of his dullness he is not successful. Another grandparent may have had natural quickness and intelligence, but also laziness and lack of ambition. Some of the grandchildren may get from one of these grandparents the genes that yield industry and ambition, from the other those that yield quickness and high intelligence. In this way superior individuals will be formed; men that make a success of life. Other grandchildren will get the genes for dullness, slowness, laziness and lack of ambition, all combined; these are the ne'er-do-wells, the failures. And similar new combinations will be made with respect to all sorts of characteristics.

The two methods of recombining genes are in large measure the origin of exceptional individuals, both superior and inferior. From the same set of genes may be produced, by combining them in different ways, superior individuals, mediocre individuals, and inferior individuals, all of them in various diverse types. This may be illustrated by representing the different genes in the pairs by different letters. We may represent adjacent pairs of genes in the strings by $\left\{\begin{matrix} \mathrm{A,\ B,\ C,\ D,} \\ \mathrm{a,\ b,\ c,\ d} \end{matrix}\right.$ and may assume that the four genes represented by the capital letters are superior and dominant, those represented by the lowercase letters defective and recessive. Suppose that there are four individuals, all having the gene combination $\left\{\begin{matrix} \mathrm{A,\ B,\ C,\ D.} \\ \mathrm{a,\ b,\ c,\ d} \end{matrix}\right.$ All of these will be of highest possible type, since all have one of the superior and dominant genes to each pair. But with the same genes differently combined we might have the four individuals $\left\{\begin{matrix} \mathrm{A\ B\ C\ D,} \\ \mathrm{A\ B\ C\ D,} \end{matrix}\right. \left\{\begin{matrix} \mathrm{A\ B\ C\ D,} \\ \mathrm{A\ B\ C\ D,} \end{matrix}\right. \left\{\begin{matrix} \mathrm{a\ b\ c\ d,} \\ \mathrm{a\ b\ c\ d,} \end{matrix}\right. \left\{\begin{matrix} \mathrm{a\ b\ c\ d.} \\ \mathrm{a\ b\ c\ d} \end{matrix}\right.$ Here two of the individuals are of the highest type, two of the lowest (since all their gene-pairs have defective genes). Again, with the same set of genes still differently combined we may have the four individuals $\left\{\begin{matrix} \mathrm{A\ b\ C\ D,} \\ \mathrm{A\ b\ C\ D,} \end{matrix}\right. \left\{\begin{matrix} \mathrm{a\ B\ c\ D,} \\ \mathrm{a\ B\ c\ D,} \end{matrix}\right. \left\{\begin{matrix} \mathrm{A\ B\ c\ d,} \\ \mathrm{A\ B\ c\ d,} \end{matrix}\right. \left\{\begin{matrix} \mathrm{a\ b\ C\ D.} \\ \mathrm{a\ b\ C\ D} \end{matrix}\right.$ All these are superior with respect to some of their gene-pairs, defective with respect to others; and the combination of superior and defective characteristics manifested will be different in each of the four. A great number of other combinations can be made of these same genes, shifted in different ways. Any one of these sets of four combinations may be converted into any other of the sets, by such recombinations as occur in reproduction from two parents. Multiply by hundreds the numbers of diverse pairs of genes, and also the number of existing individuals; we have then the situation found in an organism. The number of diverse combinations of genes that may be produced is practically infinitely great; far greater than is ever completely carried out in the production of developed individuals.

Likeness and Unlikeness of Parents and Offspring

But may not parents produce offspring that are like themselves? Heredity usually does not mean complete likeness, as we have seen, for there are many ways in which new combinations of genes are produced at reproduction. May heredity at times mean complete likeness between parent and offspring?

Parents having a certain type of genetic constitution will produce children having the same constitution as themselves. But such parents are rare; they probably never occur in man. In order that parents may give offspring of the same genetic constitution as themselves, two conditions must be fulfilled. First, the two parents must have identically the same genes, pair for pair; the entire genetic system of the one parent must be a precise replica of that of the other. This condition is fulfilled by two individuals that are identical twins; but as these are always of the same sex, they are never joint parents of the same offspring. Second, each of the two like parents must have the two members of each pair of his genes alike, so that his two sets of genes—that which came from his father, and that from his mother—are exactly alike. This condition is beyond doubt never fulfilled in man, and rarely, if ever, in any of the higher organisms. In lower animals and plants an approach to it may be brought about by many generations of inbreeding, in which the closest possible relatives are successively mated.

The required situation may be illustrated by representing the members of the pairs of genes by letters of the alphabet, capitals signifying dominant genes, lower-case letters recessive genes. Then two parents that yield offspring having the same constitution as themselves must show such identical gene combinations as the following:

$$\left\{\begin{matrix}\text{A B c D e F,} \\ \text{A B c D e F,}\end{matrix}\right. \text{ mated with} \left\{\begin{matrix}\text{A B c D e F.} \\ \text{A B c D e F}\end{matrix}\right.$$

As will be seen, when from each of two such parents one gene of each pair is taken, and the two so taken are combined to form new pairs for the offspring, the gene-pairs of the offspring will have exactly the same constitutions as those of the two parents; namely $\left\{\begin{matrix}\mathrm{A\ B\ c\ D\ e\ F.}\\ \mathrm{A\ B\ c\ D\ e\ F.}\end{matrix}\right.$ If there were a race of organisms constituted in this way, all its individuals would be alike in their genetic constitutions. Any differences between them would be the result of the action of diverse environmental conditions. If we compared two diverse races, each constituted in this way and each reproducing in this manner, heredity would mean likeness throughout; each race would be uniform and constant in its hereditary constitution, and uniformly different from the other race (save insofar as this was prevented by diverse environments). This condition is apparently nearly or quite realized in the case of certain plants that fertilize themselves. It may be approached in some strains of domestic animals. But in species in which mating occurs freely among the different types of individuals, this condition is not even approached. In man, two parents are always diverse in their genetic constitutions, and the two sets of genes of each parent are always diverse in their make-up. The result is that in such an organism new combinations of genes are formed at every reproduction.

It is not particularly rare for the parents to be so constituted that the children are like them in respect to particular single characteristics. Two parents may be alike in the genes that determine the color of the eyes. Two brown-eyed parents may each have the dominant genes $\left\{\begin{matrix}\mathrm{A};\\ \mathrm{A}\end{matrix}\right.$ the offspring will have these same genes, and will likewise be brown-eyed. Two blue-eyed parents may have the recessive genes $\left\{\begin{matrix}\mathrm{a};\\ \mathrm{a}\end{matrix}\right.$ the offspring will have these same genes, and will be blue-eyed. But of course two brown-eyed parents may have the constitution $\left\{\begin{matrix}\mathrm{A},\\ \mathrm{a}\end{matrix}\right.$ in which case some of their children will be blue-eyed. And even blue-eyed parents, it appears probable, may in different cases have the color due to different pairs of recessive genes, so that the two pairs of genes could be represented in the two parents as $\left\{\begin{matrix}A & b\\ A & b\end{matrix}\right.$ and $\left\{\begin{matrix}a & B.\\ a & B\end{matrix}\right.$ Then the children will have the combination $\left\{\begin{matrix}A & B,\\ a & b\end{matrix}\right.$ and, with a dominant gene in each pair, the color of their eyes will not be blue, but some dominant color. Such cases have been reported.

Similar relations will be found for all sorts of differences in characteristics that result from differences between the members of single pairs of genes. From the characteristics manifested by the parents, one cannot judge with certainty as to the make-up of their gene-pairs. Knowledge of the make-up of their gene-pairs is acquired mainly from observation of the kinds of offspring produced by them. But also, records of the characteristics of the ancestors of a given individual for some generations back will throw light on the genetic constitution of that individual. If we wish to know beforehand what types of offspring (with respect to particular characteristics) any particular parents are likely to produce, we must depend on these records of the characteristics of their ancestors.

Thus, if a brown-eyed individual is derived from one brown-eyed parent, and one blue-eyed parent, we know that in him the gene-pair in which the parents differed is made up of one dominant gene giving brown eyes, one recessive gene that by itself would give blue eyes; that is, the pair is of the type $\left\{\begin{matrix}A.\\ a\end{matrix}\right.$ On the other hand, if a brown-eyed child is derived from two brown-eyed parents, in him the particular gene-pair may be either $\left\{\begin{matrix}A\\ A\end{matrix}\right.$ or $\left\{\begin{matrix}A,\\ a\end{matrix}\right.$ and there is no way to determine which it is, except from the eye colors of the different children produced by this individual, when mated with another parent having eyes of one of the recessive color types. Similar situations confront us with respect to any single characteristics. By precise family records extending back for several generations prediction is made more secure; but in many cases there can be no certainty, until after a number of offspring have been produced.

By what means could a race be produced that would be constant and uniform; a race in which the offspring would be like the parents in genetic constitution?

As we have seen, there are two requirements for this: (1) The two sets of genes of each individual must be alike; each gene-pair must have two like genes. (2) The different individuals must be throughout alike in their gene-pairs.

This situation can be approached only by mating of close relatives for generation after generation; by long continued inbreeding. This will tend to bring about fulfilment of the first condition mentioned above, causing the two sets of genes of a given individual to be alike. The second required condition, that the different individuals shall be alike in their genes, can be met by combining rigid selection with inbreeding; by keeping only individuals that are closely alike in their characteristics, and rejecting all the rest. How this works may be simply illustrated by considering only two pairs of genes. Suppose that with respect to the two pairs the original parents have the constitution $\left\{\begin{matrix}A\ B\\A\ B\end{matrix}\right.$ and $\left\{\begin{matrix}a\ b\\a\ b\end{matrix}\right.$ respectively. Their children have then the constitution $\left\{\begin{matrix}A\ B.\\a\ \ b\end{matrix}\right.$ Now we mate together some of these children. From each pair one of the genes is taken, and those from the two parents are put together to give the offspring. In this way, from parents $\left\{\begin{matrix}A\ B\\a\ b\end{matrix}\right.$ nine types of offspring are produced. These are $\left\{\begin{matrix}A\ B,\\A\ B\end{matrix}\right.$ $\left\{\begin{matrix}A\ B,\\A\ b\end{matrix}\right.$ $\left\{\begin{matrix}A\ B\\a\ B\end{matrix}\right.$ $\left\{\begin{matrix}A\ b,\\A\ b\end{matrix}\right.$ $\left\{\begin{matrix}a\ B,\\a\ B\end{matrix}\right.$ $\left\{\begin{matrix}a\ B,\\a\ b\end{matrix}\right.$ $\begin{matrix}A\ b,\\a\ \ b\end{matrix}$ $\left\{\begin{matrix}AB,\\a\ \ b\end{matrix}\right.$ $\left\{\begin{matrix}\ \\\ \end{matrix}\right.$ and $\left\{\begin{matrix}a\ b.\\a\ b\end{matrix}\right.$ Some of them, as will be seen, fulfil the first requirement; they have the two genes of each pair alike. Such are $\left\{\begin{matrix}A\ B,\\A\ B\end{matrix}\right.$ $\left\{\begin{matrix}a\ B,\\a\ B\end{matrix}\right.$ $\left\{\begin{matrix}A\ b\\A\ b\end{matrix}\right.$ and $\left\{\begin{matrix}a\ b.\\a\ b\end{matrix}\right.$ The problem now is to recognize these individuals, and to breed together two of the same type. This can usually not be done with certainty, except for the pure recessive type $\left\{\begin{matrix} a\ b. \\ a\ b \end{matrix}\right.$ And these are frequently defective and therefore undesirable, so that they are not chosen. One is forced merely to breed together the individuals that are most alike, hoping that in some cases all their offspring will be alike, and like the parents. This commonly requires trials for many generations. Finally we may get together two such parents as $\left\{\begin{matrix} A\ b. \\ A\ b \end{matrix}\right.$ Then all their offspring will be of the same constitution. If now we reject all the other descendants and breed from these alone, we shall have a race that is uniform and constant with respect to these two pairs of genes.

Inbreeding of course is as likely to bring together defective genes, if they exist, as to bring together perfect ones. If in the example we have used, a and b are taken to represent defective genes, then by long continued inbreeding we shall get such constant defective races as $\left\{\begin{matrix} a\ b, \\ a\ b \end{matrix}\right. \left\{\begin{matrix} a\ B, \\ a\ B \end{matrix}\right. \left\{\begin{matrix} A\ b, \\ A\ b \end{matrix}\right.$ as well as the perfect ones $\left\{\begin{matrix} A\ B. \\ A\ B \end{matrix}\right.$

But in organisms we must deal not with merely two pairs of genes, but with hundreds. This increases greatly the difficulty of the problem. Inbreeding must be continued for many generations, and in every generation rigid selection must be practiced. Most of the offspring produced must be rejected, and only those most alike retained and bred together. Even after many generations of such inbreeding, the race will as a rule be found still to lack uniformity in some or many gene-pairs; so that it is not constant in its hereditary constitution. Parents will still give offspring unlike themselves in some respects.

In certain plants self-fertilization occurs in every generation; the same individual furnishes both the germ cells that unite to form a new individual. This is the closest form of inbreeding. In such plants it has occurred for hundreds of generations in succession. In consequence the diverse races of such plants show each a high degree of constancy and uniformity in its members. If in man we were dealing with organisms of this kind, none of the surprises and paradoxes of inheritance, described in previous pages, would occur. Wise men would produce wise children, fools would produce fools, knaves would yield knaves; each type of parent would have children of the same type as himself—in features, in physiology, in mentality. Society and its problems would be very simple compared with the condition that we actually find.

For in most organisms, including man, inbreeding is not the rule. In many of them there are special conditions that prevent the mating of close relatives. In man, as we know, the mating of close relatives is in most races prevented by customs and laws. As we saw on an earlier page, mating of close relatives brings out hidden defects in the genes, while mating with unrelated individuals keeps these defects concealed. This is doubtless the biological ground for the avoidance of inbreeding; human beings do not wish to produce defective offspring. If there were no defective genes, there would be no biological objection to inbreeding.

In man and the higher animals in which inbreeding is not the rule, the individuals are very diverse in their genetic constitutions, and consequently the offspring have gene combinations very different from those of their parents. They may therefore differ from their parents in many of their characteristics. From vigorous and efficient parents may be produced offspring that are weak and inefficient; from defective parents may be produced offspring that are perfect, in the ways set forth on earlier pages. Superior individuals are the result of particularly fortunate combinations of genes; inferior individuals that of unfortunate combinations.

From this point of view, human society may be divided roughly into three classes. At the top, forming a small percentage of all, are the superior individuals, with good combinations of genes, their defective genes protected by normal ones. At the other extreme is another small class, of the inefficient, the criminal, the undesirable, having poor combinations of genes, their defective genes not protected by others. Between them lies the great mediocre class, comprising 95 per cent of the population. A large majority of the members of the two extreme classes arise from parents of the mediocre class. When from such parents fortunate combinations are made, with the genes supplementing each other, children are formed that pass into the superior class. These are individuals whose names get into Who's Who; they are poets, inventors, men of science, oil kings, baseball magnates. When a bad combination is made, the children fall back into the inferior or undesirable class; they are vagabonds, criminals, paupers. A new combination is made with every child, and any single pair of parents can form literally thousands of diverse combinations. So from the same parents some of the children may fall in the superior group, some in the mediocre group, some in the inferior group. Prediction cannot be made as to where a particular child will fall.

The frequent appearance of offspring that do not resemble the parents and do not resemble each other, is not an indication of the failure or weakness of inheritance, if we mean by inheritance dependence of the individual's peculiarities on the genes that he receives from his parents. On the contrary, the appearance in a family of a child differing greatly from parents and brethren, though brought up in the same household and by a similar system of treatment, is, if rightly understood, a striking instance of the power of the genes to influence human life and characteristics. A dead level of similarity in the family would be unintelligible from the genetic point of view; would be incompatible with what we know of the operation of the genetic system in higher organisms.

But in all this change from generation to generation, in all this recombining of genes, with consequent production of diverse sets of characteristics, is there no tendency at all for parents to produce children that are like themselves? Is there not on the whole some heightened degree of resemblance between the members of families?

Of course there is. In spite of all exceptional cases, the members of a particular family resemble each other, on the average, more than do an equal number of individuals picked up on the street at random. If we choose a lot of parents that are blue-eyed, they will be found to have produced a greater proportion of blue-eyed children than will a selected lot of brown-eyed parents. A lot of tall parents will be found to have produced a greater proportion of tall children than have a lot of parents of low stature. With respect to physical characteristics, all these things can be measured; degrees of resemblance can be expressed numerically. Parents and offspring show a considerable degree of correlation in their physical characteristics; so also do the different children of the same family. The coefficient of correlation is about 40 to 50 per cent, between members of the same family—that between individuals taken at random being zero, and that between individuals exactly alike (if such existed) being 100 per cent. These relations are matters of averages for large numbers of individuals. For any particular individual in his relations to parents or brethren, prediction is most unreliable.

Expressed with reference to the genes, these relations signify that, on the whole, members of the same family have more genes in common than have sets of individuals taken at random. Or more precisely, members of the same family have in common more *manifested* genes than have a set of individuals taken at random. By manifested genes we may signify those genes that are producing their characteristic effect: the dominant genes when both dominants and recessives are present in the same pair; the recessive genes when recessives are the only type present. In brown-eyed persons the dominant gene is the manifested one, though the recessive gene may be present also; in blue-eyed persons the recessive gene is the manifested one, since no dominant gene for eye color is present. The fact that close relatives or members of the same family, have in common more manifested genes (on the average) than have unrelated individuals, can be demonstrated. It follows that, other things being equal, close relatives resemble each other more, on the average, than do unrelated individuals, in respect to any characteristics whatever that depend on genes, whether structural, functional or mental. This relation may be disturbed in particular groups through differences in environmental conditions, since functional and mental characteristics are deeply affected by differences in environment—a matter to be dealt with in later chapters. But in the long run the greater similarity of closely related individuals in respect to all kinds of characteristics that depend on genes is bound to show itself.

What Kinds of Characteristics Depend on Genes?

Finally, what kinds of characteristics depend on genes? That is, what kinds of characteristics are altered by altering genes, by substituting one or more genes for others, in the genetic system?

To this the answer must be that all types of characteristics, all manifestations of life, of whatever sort, are alterable by altering genes. Experimental genetics has certainly gone far to demonstrate this proposition. Structural characteristics, internal and external, colors, shapes, sizes, chemical properties, physiological functions, senses, behavior—all have been shown to be changed by changing genes.

And this is not surprising. What it means is simply that by changing the material of which an individual is made, any or all of his properties, all his characteristics, may be changed; just as by changing the materials of which the parts of an automobile are made, any or all of its characteristics, including the way it runs, may be changed. It would be surprising if this were not so, both for the machine and for the organism. The fact that this is true has no bearing on the question whether there are not also other ways of changing the characteristics. In the case of the machine, its properties and performance may also be changed by altering the method of manufacture; by altering the conditions to which the material is subjected, the processes through which it is put. It would seem probable that the same should be true for organisms. With this matter we deal in later chapters; particularly Chapter V, where we take up explicitly the question: What differences in the characteristics of organisms may be made by altering the conditions under which they develop; by altering the environment?

NOTES AND REFERENCES ON CHAPTER I

Detailed descriptive accounts of the matters dealt with in Chapter I will be found in the modern text-books of Genetics. Among these are: *The Physical Basis of Heredity,* by T. H. Morgan (Philadelphia, 1919); *How We Inherit,* by E. Altenburg (New York, 1928); *Genetics in Relation to Agriculture,* by E. B. Babcock and R. E. Clausen (New York, 1927); *Genetics and Eugenics,* by W. E. Castle (Cambridge, Mass., 1924).

1. Page 21. See Castle, *The Explanation of Hybrid Vigor.* Proceedings of the National Academy of Sciences, Vol. 12, pp. 16–19.

II

HOW DO WE KNOW THAT GENES ARE REALITIES? HOW DO WE KNOW THAT THEY AFFECT CHARACTERISTICS?

Nature of the Evidence

How do we know that genes exist; and that they affect characteristics in the way set forth in earlier and later chapters? How secure is this knowledge? How were these matters discovered, and what is the nature of the evidence for them? What are the demonstrable relations between genes and characteristics?

The evidence on these matters is experimental in character; it is positive, inescapable, conclusive. But it deals with matters unfamiliar to most, and it emerges from a mountain of details that cannot be mastered without great labor. It is to this fact that the persistence of skepticism in some individuals is due. They have not mastered this mountain of evidence; otherwise their skepticism would vanish.

If genes are realities, and if they do the work attributed to them, they do not yield in interest to electrons, to atoms, or to any other constituents of the universe. From their action in development come human beings. Their behavior gives us the phenomena of inheritance; the "laws of heredity" are the rules of their distribution. Alterations in their constitution give us organic evolution. Detailed knowledge of their properties and ways is the key to the understanding of much that is most important in organisms. Temperament, mentality, behavior, personality—these things depend in manifold ways on the genes. If the genes are realities, it is vain to attempt to understand these matters without close attention to their properties and behavior.

What is the evidence that they are realities?

Not everyone can master in full the detailed evidence; life is too short, and other things must be done. But a sample of this evidence can be presented, and from this its nature can be judged. Here will be set forth, therefore, some of the striking facts and relations, that illustrate the nature and decisiveness of the evidence for the existence of genes and for their relation to characteristics. They include many of the most important features of heredity.

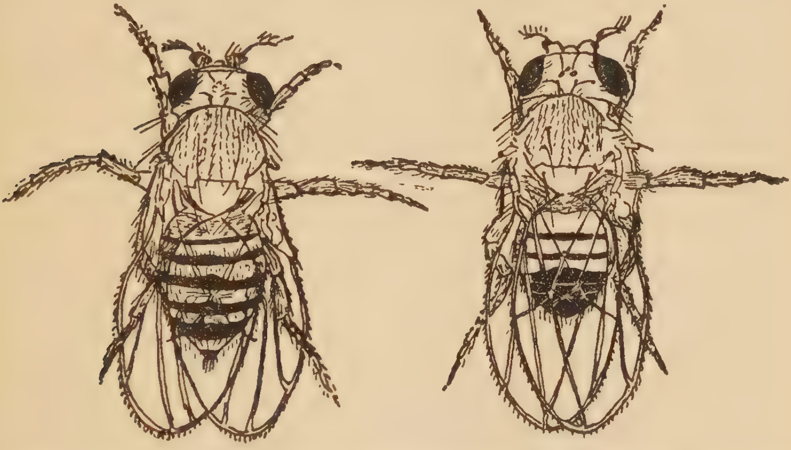


Figure 14—The fruit-fly, Drosophila melanogaster, on the study of which much of our knowledge of heredity is based. Female to the left, male to the right. After Morgan, Bridges and Sturtevant, The Genetics of Drosophila.

Much of this evidence has come from the great investigations of Thomas Hunt Morgan and his associates on the common fruit-fly, Drosophila melanogaster(figure 14). This animal has extraordinary advantages for this type of work; so that many of the fundamental facts as to inheritance and its relation to genes were first discovered in this creature. These have since been confirmed for many other organisms, so that the conditions found in the fruit-fly are, in essentials, of rather general validity. Many of our illustrative facts will be taken from the fruit-fly.

The Clue: the X-Chromosome and the Characteristics that Follow It

The clue that finally unraveled the whole tissue of relations, and made it possible to place all on a solid experimental basis, was the discovery that in many higher organisms the individuals of the two sexes differ at the very beginning of their existence, one sex having one more chromosome than the other. This additional chromosome is transferred, as generations pass, from individuals of one sex to those of the other, and back again, in a systematic and characteristic way. This made it possible to trace with certainty from generation to generation the course of a particular chromosome. And therefore it was possible to discover whether any of the distinctive characteristics of particular individuals follow that particular chromosome, as it is transferred from parent to offspring. In this way it was found that not only single characteristics, but entire groups of separable characteristics thus follow the course of a single chromosome. They follow it in its typical course from generation to generation; a course so characteristic and remarkable (as will be shown later) that it cannot be mistaken. They follow it equally when accident makes the particular chromosome take an abnormal course. This discovery became the key to the whole matter. Following it up, there was traced the entire system of the relation of characteristics to chromosomes, and to their constituent parts, the genes.

To appreciate how this was done, some details regarding the chromosomes, and regarding their relation to sex, must be grasped. The chromosomes are plainly seen under the microscope. Although for practical purposes they are usually made more conspicuous by coloring them with dyes, it is important to understand that they are visible in living cells, without aid from dyes.[1]

In certain higher animals, notably in certain insects, it was found that a female individual has, at the very beginning of its existence, when it is but a single cell, one more chromosome than a male. The female has an even number of chromosomes, constituting a certain number of pairs—the two members of each pair being alike in size and form (figure 15, B). The male has an odd number of chromosomes, one of its "pairs" having but a single member (figure 15, A) in place of the two found in the female. The odd chromosome of the male was designated X. It soon appeared, as we shall see, that the pair in the female corresponding to this X is composed of two of the X's—two that may in earlier generations have existed in males, as the odd chromosome. That is, the male contains a certain number of pairs of chromosomes, plus one X; the female contains the same number of pairs, plus two X's (these constituting another pair).

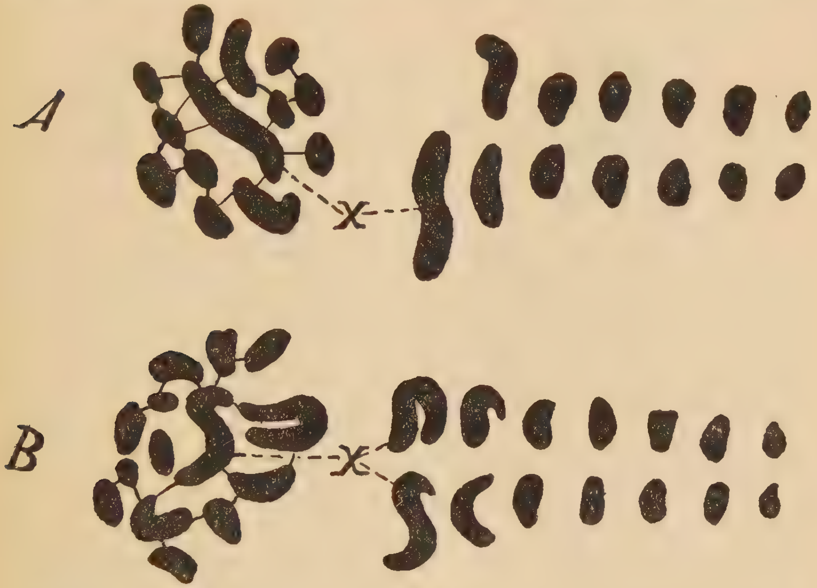


Figure 15— The male (A) and female (B) groups of chromosomes in a bug, Protenor, after Wilson. At the left in each case is shown the group of chromosomes as it appears under the microscope. At the right are shown the pairs of chromosomes constituting the group, arranged in order of size.

In many other species, including man, the male has, as mate to the single X, another small chromosome, known as Y (figure 16). This chromosome Y is rudimentary; it is usually

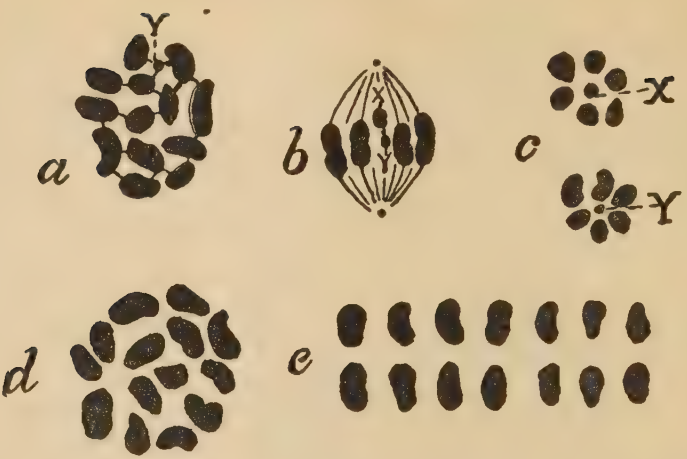


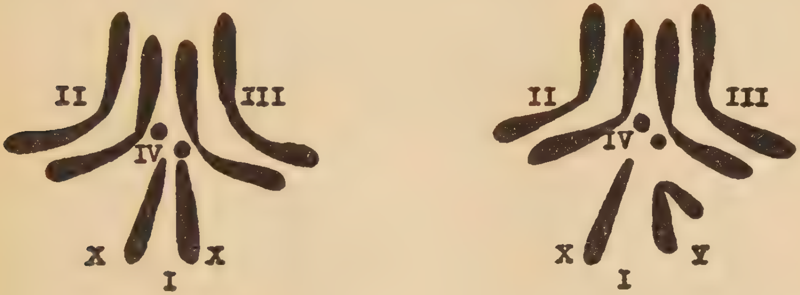
Figure 16—Male and female groups of chromosomes in an animal (Lygaeus) in which the male has a Y chromosome, after Wilson. a, The male group of 14 chromosomes as seen under the microscope; b, the process of division of this group into two groups of seven chromosomes each, in forming germ cells. c, The two groups of seven chromosomes in the two kinds of germ cells formed, one containing the chromosome X, the other the small chromosome Y. d, The female group of 14 chromosomes, as seen under the microscope. e, The 7 pairs constituting the female group, in order of size.

minute in size, and is found to have little function. It does not occur in the females, but is found exclusively in males. In some species this Y, though rudimentary in function, is nearly or quite as large as X, but of a different form; this is the case in the famous fruit-fly (figure 17), in which these matters have been most completely studied.

Thus in these organisms male and female differ in their chromosomes at the very beginning of their existence as individuals, when they are single cells. When the cells divide, so as to produce finally the body of the adult, at every division each of the chromosomes divides into two, one half passing into each of the cells produced. So every cell of the body has the same set of chromosomes that was present at the beginning, in the single cell of the fertilized egg. In the male therefore every cell of the body differs in its chromosomes from every cell of the female body.

This situation made it possible to trace particular X-chromosomes from a certain parent to a certain one of the offspring, and so to discover whether one X-chromosome differs in effects from another. This is done in the following way:

When the parent produces the germ cells that are to give rise to the next generation, each germ cell receives one member of each pair of the parent's chromosomes (figure 18).



Female **Male**

Figure 17—The groups of chromosomes of the two sexes in the fruit-fly, Drosophila melanogaster. The female group at the left, with two straight X-chromosomes; the male group at the right, with one straight X and one bent Y. After Morgan, Bridges and Sturtevant, The Genetics of Drosophila. The roman numerals are the designators commonly employed for the different pairs, the two X's (or X and Y) constituting pair I.

Thus the germ cell contains half as many individual chromosomes as did the cells of the body of the parent. In males, some of the germ cells (or sperms) receive the X-chromosome, others do not (figure 18,A). Thus the male produces two kinds of germ cells, one containing the X-chromosome, others without it. (The latter contain the rudimentary Y-chromosome, in species that have a Y-chromosome.)

The germ cells from the female show no such division into two classes. Since there is in the female parent a pair of X's, each germ cell, or ovum, receives an X; all the ova therefore have one X each (figure 18, B).

Now fertilization occurs, by the union of a sperm with an ovum. When a sperm bearing an X unites with an ovum (also bearing an X), the resulting fertilized egg has of course two X's. It therefore develops into a female individual (figure 19, B). But when a sperm having no X (though in some species bearing a Y) unites with an ovum, the resulting fertilized egg has but one X (with or without a Y); it therefore develops into a male (figure 19, A).

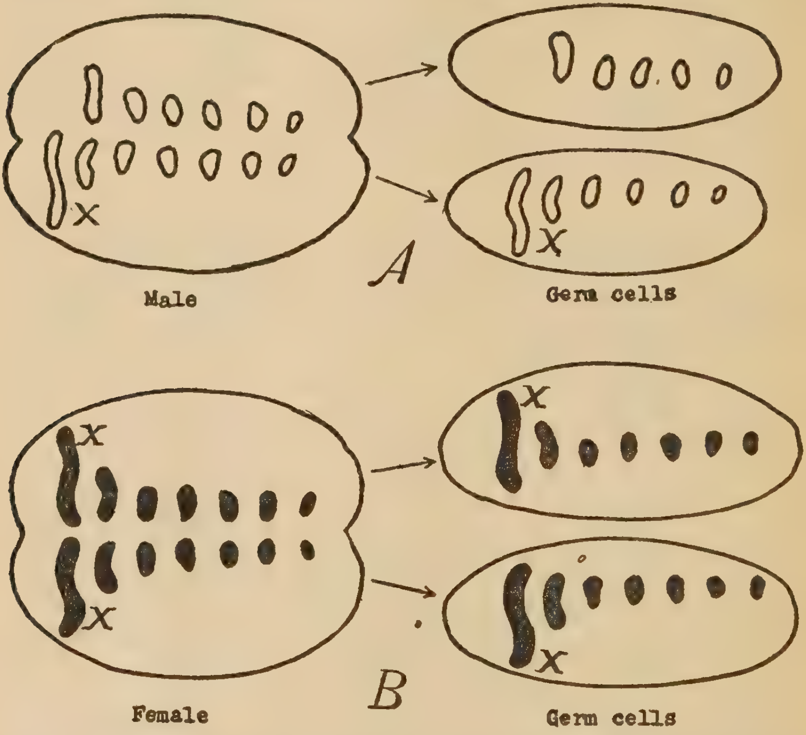


Figure 18—Diagrams to illustrate the chromosome combinations in the formation of germ cells, in males and females. The chromosomes of Protenor (Figure 15) are employed as the basis of the diagram. The chromosomes of the male are represented in outline, at A; the chromosomes of the female in solid black, at B. At the left in each case is represented a cell of the parent individual, in the male with six pairs of autosomes and one X; in the female with six pairs and two X's. At the right are the germ cells. Half the germ cells from the male have an X, half do not; while all the germ cells from the female have an X. (See figure 19 for continuation of this diagram.)

From this it will be seen that the X-chromosome of a father always passes to his daughters, never to his sons; also that a son always gets his single X-chromosome exclusively from his mother, never from his father; and this continues for generation after generation. If therefore the X-chromosomes from the original mother produce a different effect, a different characteristic, from the X-chromosome of the original father, it will be possible to trace these diverse characteristics by following the course, for generation after generation, of the different

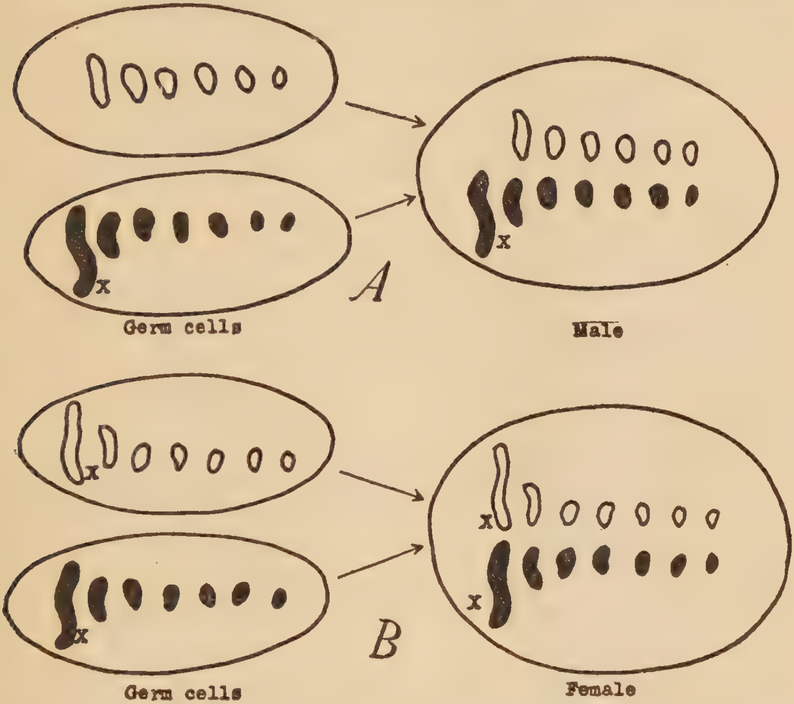


Figure 19—Continuation of diagram of figure 18. Formation of male and female individuals (fertilized eggs), by the union of germ cells from the male and female parents. Chromosomes from male represented in outline, from females solid. A, formation of a male individual, by union of a male germ cell bearing no X, with a female germ cell that bears an X. B, formation of a female, by union of a male germ cell bearing X with a female germ cell likewise bearing X. The X-chromosome of the male thus goes only to his daughters, not to his sons.

X-chromosomes. Any effect produced exclusively by the father's X-chromosome may appear in his daughters, but not in his sons. Any effect produced exclusively by the mother's X-chromosome must appear in her sons (since they have only this type of X) ; and may or may not appear in the daughters, since these have both types of X's, and in some cases one may be dominant, in other cases the other.

Characteristics that Follow Chromosomes Having a Particular Origin

Making use of these facts, it was found that often the father's X-chromosome does indeed produce a different effect from the mother's X-chromosome. A typical case will illustrate this; it shows the relations found for hundreds of different characteristics. In the fruit-fly there occur individuals in which the eye is abnormal in structure, having many of its facets incompletely developed, so that the complete facets form a broad "bar" across the eyes (figure 20). If a male that is bar-eyed is mated with a female with normal eyes, all his daughters have the abnormal bar-eyes, while all his sons have normal eyes (figure 20). That is, all the children that contain the X from the father have the bar-eyes; all those that do not contain this X, but only the X from the mother, are without the bar-eye abnormality.

But if we mate a female that has bar-eyes with a male that is normal, all the children—both sons and daughters—have bar-eyes. The sons get their X from the mother; and the daughters also get one of their X's from their mother. Thus all the children now get an X from the abnormal parent, and all have the abnormality.

It looks therefore as if this bar-eye abnormality may be due to a peculiarity of certain X-chromosomes; while other X-chromosomes are without it. And this is confirmed by all the further experiments that are made. As seen above, if the father has the bar-eye while the mother has not, all the daughters have the bar-eye (figure 20). We know that these daughters

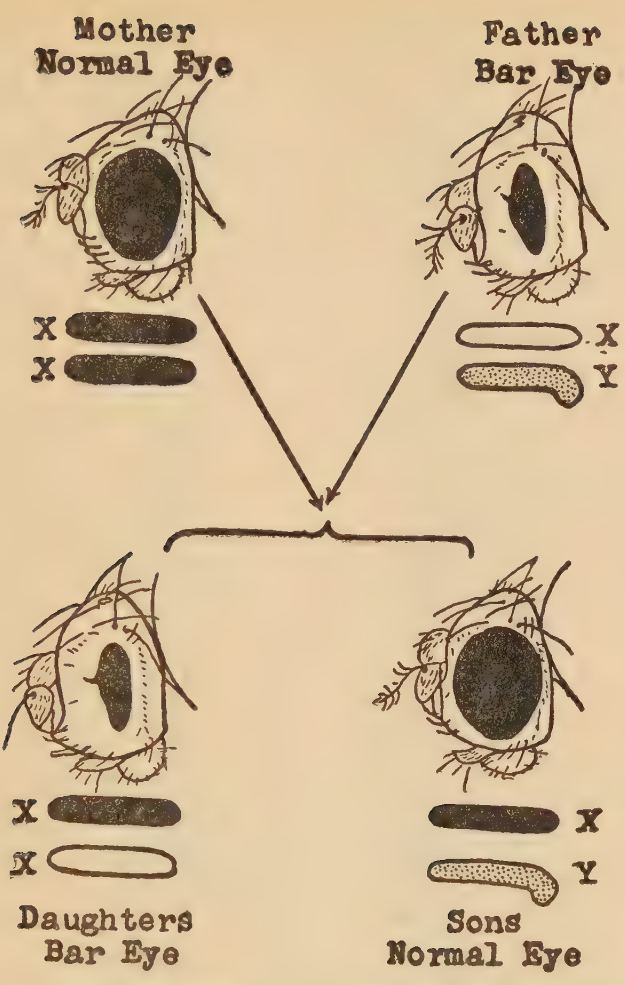


Figure 20—Bar-eye and normal eye, in Drosophila, and their method of inheritance when a mother with normal eyes is mated to a father with bar-eyes. The dark area in each eye represents the region occupied by normal facets of the eye; in the bar-eyed individuals (upper right and lower left), this is reduced to a narrow bar. Below each figure of the eyes are shown the X-chromosomes of the individual; those of the mother (normal) being shown in black; that of the father (defective) being shown in white. The Y-chromosome is stippled. In the daughters and sons, the X-chromosomes derived from the mother are shown in black, those from the father in white. All individuals that have an X of the paternal type (white) have the bar-eye. In consequence the daughters are like the father, the sons like the mother.

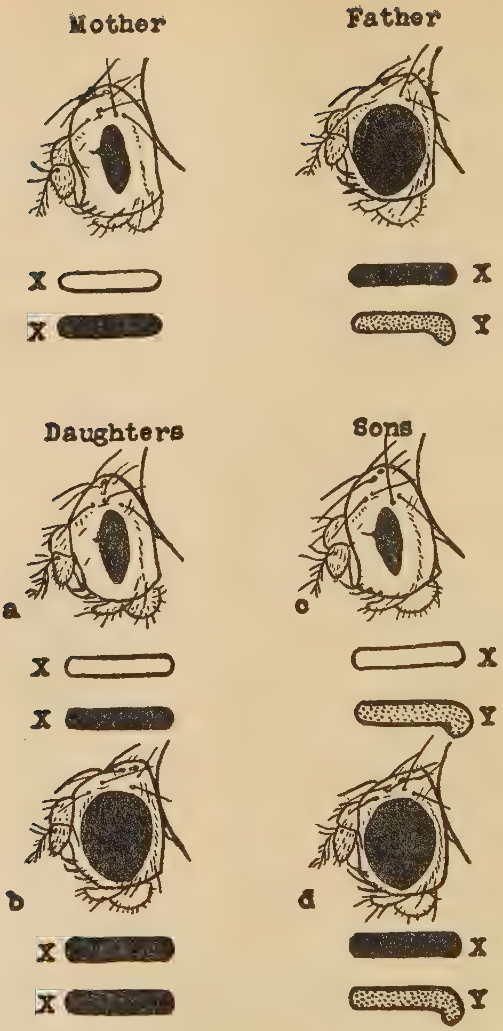


Figure 21—Inheritance when one of the daughters of figure 20 is the mother, and the father has normal eyes. The mother has one of the X-chromosomes that produce bar-eye (outline), one that does not (black); the father's X is of the type that does not produce bar-eye. Of the daughters, half (a) receive the chromosome that produces bar-eye, half (b) receive the other chromosome; the former (a) have bar-eyes, the latter (b) do not. Also half the sons (c) receive from the mother the bar-eye chromosome, while the other half (d) do not; the former have bar-eye, the latter normal eyes.

have one X from the father, one from the mother (figure 19, B). Mate such daughters now with a male that has normal eyes (figure 21). We find that half the sons and half the daughters have bar-eyes, while the other half have normal eyes. And we see also that half the sons and half the daughters

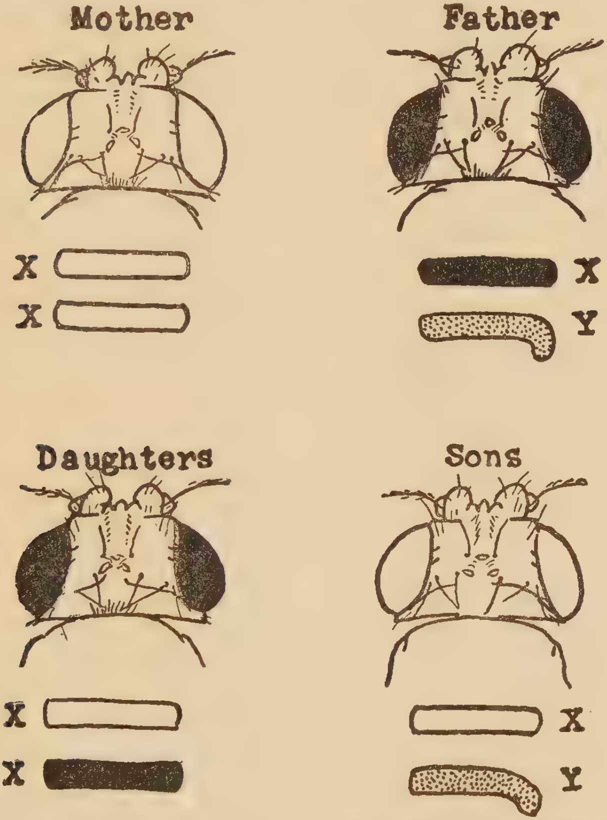


Figure 22—Inheritance of a recessive characteristic that depends on a particular type of X-chromosome: white eyes. The mother has white eyes (represented in outline), the father red eyes (represented in black). The chromosomes of each individual are represented below the figure of its head, the mother's chromosomes in outline, the father's in black. The daughters, receiving one X-chromosome from each parent, have red eyes, like the father. The sons, receiving an X-chromosome from the mother only, have white eyes, like the mother (the Y-chromosome having no effect on the eyes). The white eyes appear wherever the maternal type of X (outline) is the only type of X that is present.

have received the X that came originally from the bar-eyed grandparent, while the other half have not.

In whatever way we make the test the results are consistent. Children that receive an X from the bar-eyed ancestor have bar-eyes; children that receive an X from the normal ancestor have normal eyes. The bar-eye invariably follows the course of a particular X-chromosome and its descendants, occurring only where that X-chromosome is present. This is a statement of positive fact. It is clear that the bar-eye is the result of a peculiarity, a defect or abnormality, in some of the X-chromosomes. Any individuals that get such an X-chromosome have the abnormal eyes. That is, this defective X-chromosome causes the fertilized egg so to develop as to give rise to an individual with bar-eyes.

Other X-chromosomes are found to have other effects. Some of the resulting characteristics behave just as does bar-eye; they appear wherever a particular sort of X-chromosome is present; not elsewhere.

Others behave in a somewhat different manner, acting as recessive characteristics instead of as dominants. Such recessive characteristics are commoner than dominants. They all follow the same rules of distribution, appearing in any individual in which a particular kind of X-chromosome *is the only kind present.* A typical case of this sort is the following. In the fruit-fly the usual color of the eyes is red. But there occur individuals in which the eyes are white. Such white-eyed individuals when mated together produce only white-eyed offspring. But if a white-eyed female is mated with a red-eyed male, the sons all have white eyes, while the daughters all have red eyes (figure 22). The sons, we know, get their X's from their mother; and they have eyes like their mother. The daughters get one of their two X's from the mother, one from the father. Since they have eyes like their father, it appears that the father's X prevails over that of the mother. We can test whether it is the X that is responsible for the white eyes, by mating these daughters to a red-eyed male (figure 23). Now half their sons have white eyes. The sons received their single X's from their

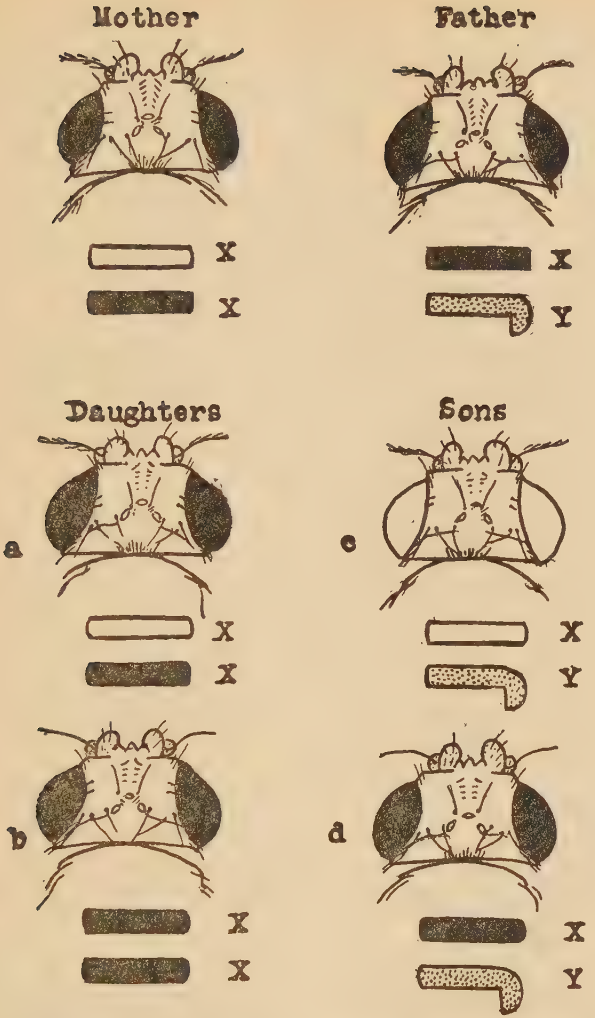


Figure 23—Course of inheritance of a recessive character (white eyes) dependent on a particular type of X. The mother has one defective X-chromosome (shown in white), derived from the white-eyed mother of figure 22, the other X-chromosome being normal (black); she therefore has normal red eyes. The father has a normal (black) X-chromosome, and normal red eyes. Of the four types of offspring shown (a, b, c, d), only one (c), representing half the sons, have the white eyes, this in consequence of their receiving the mother's defective X-chromosome. All the daughters (a and b) and the other half of the sons (d) have normal red eyes, since they contain at least one of the normal X-chromosomes.

mother, and as we know, half the X's of the mother came from the white-eyed grandmother, the other half from the red-eyed grandfather (figure 22). Those individuals that have only an X from the original white-eyed grandparent have white eyes. Those that have both sorts of X's show only red eyes.

Thus white eye is due to a certain kind of X-chromosome, but it appears only when that kind of X is the only kind present. It is a recessive character, while bar-eye, likewise depending on certain kinds of X-chromosomes, is a dominant character. Such recessive characters appear in females (where there are two X's) only if both the X's are of the same type. In the case of white eyes, if we mate red-eyed females that have one X from the white-eyed father with white-eyed males, as in figure 24, half the daughters (as well as half the sons) are white-eyed. These daughters, as figure 24 shows at *a,* have two X's that came originally from white-eyed ancestors.

Since such recessive characteristics appear in all males that have the defective X, but in only such females as have both their X's defective, they appear in many more males than females. They have therefore been called sex-linked, or even sex-limited, characteristics. But they are not limited to either sex, though commoner in males.

Many other recessive characteristics have been found to follow a particular kind of X-chromosome, being manifested only when that type of X is the only type present. In the fruit-fly more than 50 such characteristics are known. In other organisms they likewise occur; a number are known in man. Those known in man are defects or diseases; notably hæmophilia or refusal of the blood to coagulate, so that a wound causes bleeding to death; some kinds of color-blindness; a kind of muscular atrophy known as Gower's disease, and others. All follow strictly either the rules for dominant sex-linked characters, or those for recessives. That is, some are manifested wherever a certain kind of X-chromosome is present, others only where an X of a particular origin is the only type of X present.

The result of this is that these characteristics show extraordinary rules of inheritance, which were long a great puzzle.

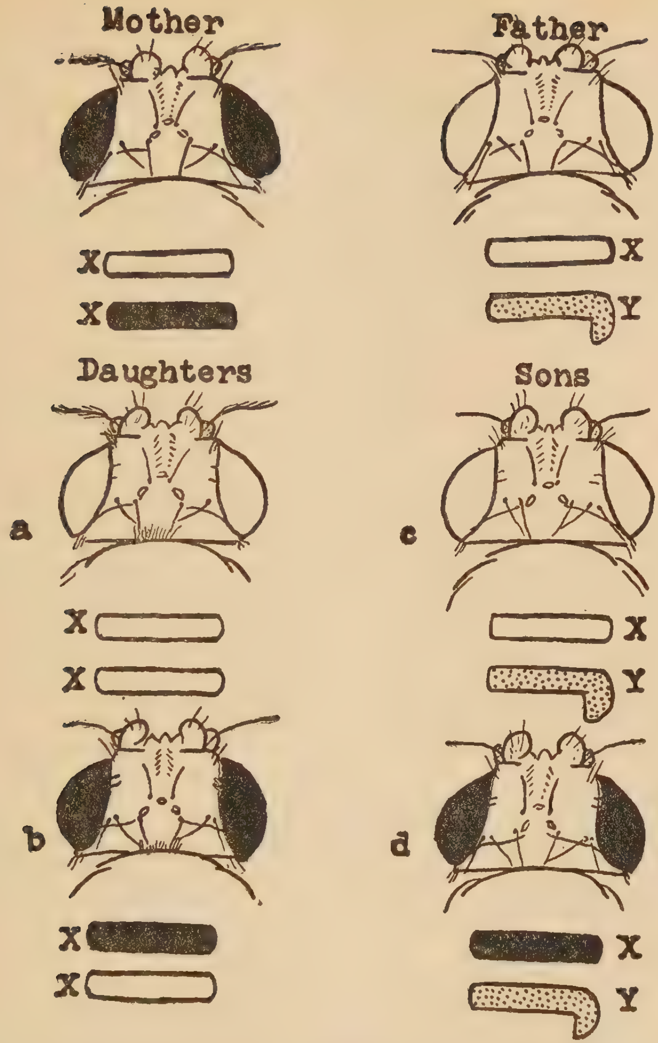


Figure 24—Course of inheritance of white eye and red eye in Drosophila, when the father has white eyes, and the red-eyed mother has one of the defective X-chromosomes (shown in white) that tend to produce white eyes. Of the daughters (a and b), one half (a) receive a defective X-chromosome from both mother and father; these have white eyes; the other half (b) receive a normal X-chromosome from the mother, a defective one from the father: these have red eyes. Of the sons (c and d), one half (c) receive the mother's defective X-chromosome, and therefore have white eyes; the other half (d) receive the mother's normal X-chromosome, and so have red eyes.

If such a characteristic as hæmophilia in man, or white eye in the fruit-fly, is followed for generation after generation, the following situation appears:

The individual showing the defect is as a rule a male. If such a defective male is mated with a normal female, none of the children are defective; the peculiarity seems not inherited. But when these children are mated with normal individuals, some of the daughters' sons show the defect; but none of the sons' children show it. Also the daughters' daughters are all without the defect. Thus, among the grandchildren, only part of the grandsons, through the daughters, show the defect that was seen in the grandfather. Further, in none of the descendants, male or female, of any of the sons, no matter how far traced, does the defect appear (unless they mate anew with a member of a defective family). This remarkable course of inheritance is illustrated in figure 25.

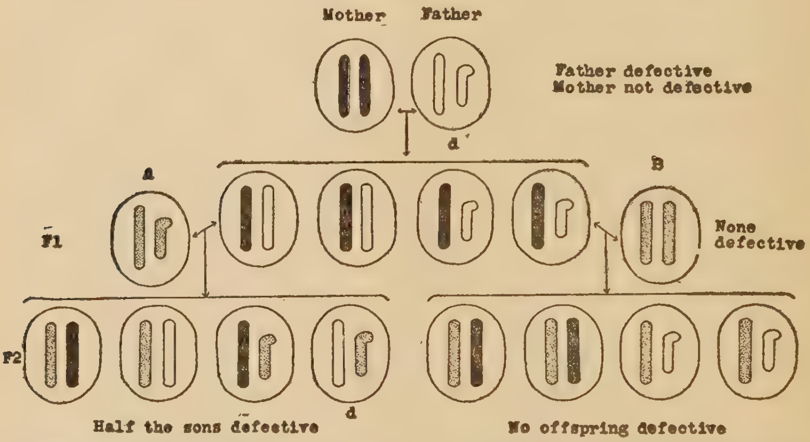


Figure 25—Diagram of the descent of a recessive defective X-chromosome, derived from the original male parent, in cases where there is outbreeding. Defective X represented in outline, normal X in solid black. The sons and daughters in F1, derived from the original mating, are conceived to mate with the unrelated individuals A and B, whose chromosomes are shown as stippled; the X-chromosomes of A and B not being defective. Defective individuals are marked *d*. In F1, none of the offspring are defective. In F2, half the daughters' sons are defective, while none of the sons' offspring (nor later descendants) are defective, since they lack entirely the defective X.

But though these are the usual rules, in very rare cases all these rules are broken. In rare cases when a defective father is mated with a normal mother, the defect appears in both the sons and the daughters. But not all the sons, nor all the daughters show it; rather only about half of them. If one of these defective daughters is mated with a normal male, all the sons

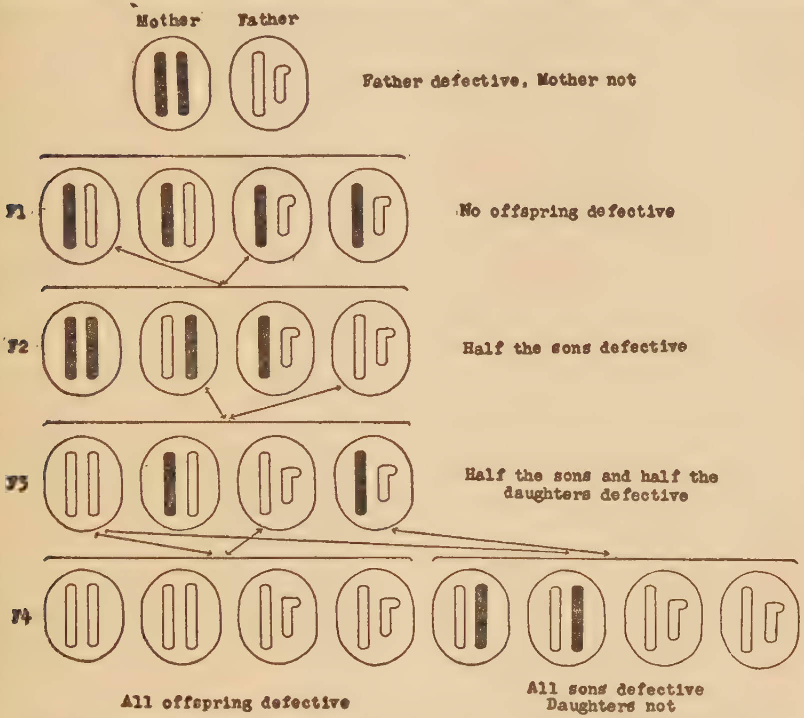

Mother
Father
Father defective, Mother not
F1
No offspring defective
F2
Half the sons defective
F3
Half the sons and half the daughters defective
F4
All offspring defective
All sons defective
Daughters not

Figure 26—Diagram to illustrate the descent for successive generations of a defective X-chromosome derived from the original male parent, when there is inbreeding among the descendants; with the various types of results produced. The defective X-chromosome is represented in outline, while the normal X-chromosomes, derived from the mother, are represented in solid black. The Y-chromosome found in males only is represented as smaller and hooked. The horizontal rows of figures represent the chromosomal conditions in the individuals of successive generations (F1 to F4) derived from the two parents at the top. Females (with two-X-chromosomes) are at the left; males (with X and Y) at the right. The arrows indicate the parentage of the successive generations. The defective X-chromosome produces a recessive personal defect; that is, individuals containing only the defective X (outline), with or without Y, are personally defective. All individuals with a normal X (black) are normal.

show the defect, while none of the daughters show it. That is, "the sons inherit from their mother, the daughters from their father."

Before the relation of the phenomena to the X-chromosomes was known, there appeared to be no consistency in such happenings. The rules of appearance of the inherited defect seemed purely arbitrary. But when one brings into relation with these the distribution of certain particular X-chromosomes, the whole matter clears up. The defect appears in individuals in which a defective X is the only type of X present; and in no others. The diagram of figure 26 illustrates all the peculiar cases set forth in the two preceding paragraphs. When the father's X is the one that is defective, while the mother's is normal, the sons get no defective X, so that none of their descendants show the effect of it (unless they mate with some individual that has a defective X). When the mother and father each have one defective X (figure 26, in F2), (so that the mother is normal, in consequence of her possession of one normal X), then half the daughters get two defective X's, and therefore show the defect; also, half the sons get a defective X, and hence show the defect. All these relations, with others, are illustrated in figure 26.

A great number of such characteristics have been studied, in many diverse organisms. Without exception they follow the distribution of particular X-chromosomes. The matter has been tested in literally hundreds of thousands of instances; all show these relations.

In rare cases the X-chromosomes are accidentally distributed in a manner different from the usual one. In such cases these "sex-linked" characteristics follow the unusual distribution of the X's. The results then are extraordinary and astonishing. It is most instructive to follow such a case:

In the fruit-fly, white eye is due, as seen above, to a defective X. A female with white eyes has two such defective X's. When such a female is mated with a normal red-eyed male, the rule is, as we have seen, that all her sons are like herself in having white eyes, while all the daughters are like the father in having red eyes (figure 22). This is because the mother gives to her ova only one of her defective X's. To produce daughters, a normal X from the father enters each

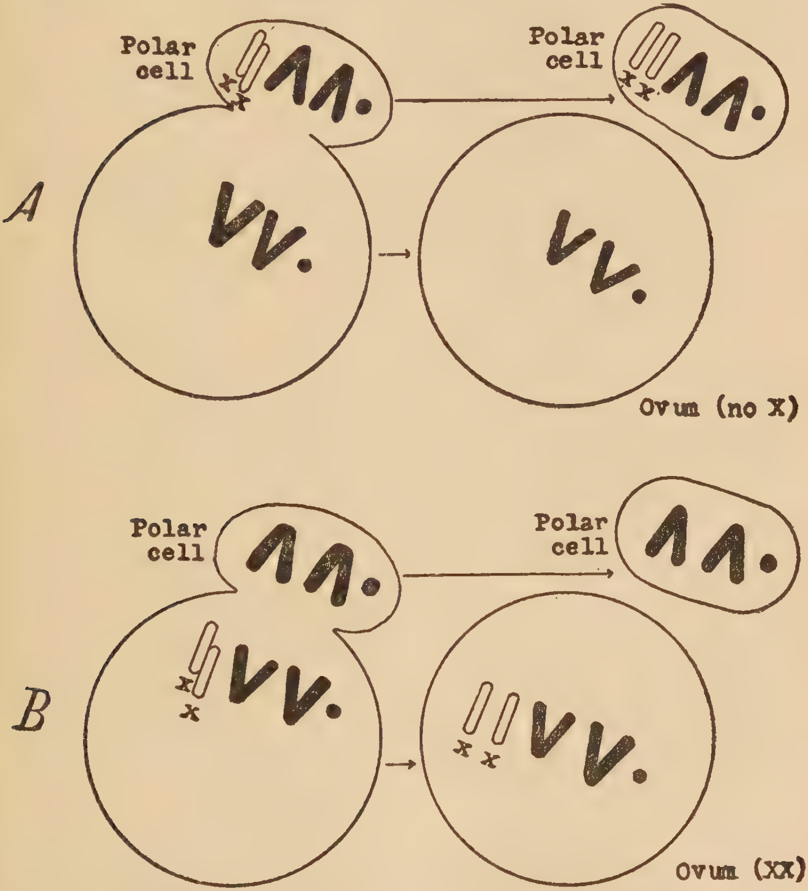


Figure 27—Diagram to show the production in Drosophila of two types of ova, in cases where the two X-chromosomes fail to separate, at the time when germ cells are formed. The X-chromosomes are represented in outline, as straight rods, the other three pairs of chromosomes (compare figure 17) in black. At A, the two X-chromosomes pass into the polar cells (rudimentary, non-functional germ cells), leaving an ovum with no X-chromosome. At B, the two X-chromosomes pass into the ovum itself, giving an ovum with one member of each of the other three chromosome pairs, but with two X's.

of these ova; the daughters are therefore normal, or red-eyed.

C. B. Bridges[2] found that in certain cases when the mother produces germ cells, her two defective X's for some reason fail to separate, so that some of the ova keep two defective X's. Others, on the other hand, get no X at all (figure 27). These two classes of ova are then fertilized by the usual two classes of sperm—one class containing an X, the other a Y. When a sperm containing a Y unites with an ovum containing the two defective X's (figure 28, A) a female is produced (though the Y sperm when it unites with an ovum containing but one X, yields a male). And now *these females show white eyes like the mother* (since both their X's are defective, coming from the mother). When a sperm containing a normal X unites with an ovum having no X (figure 28, B), a male is

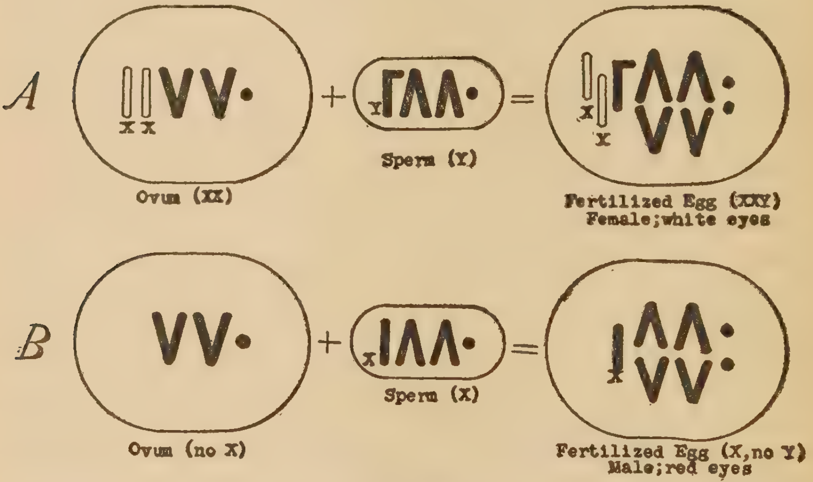


Figure 28—Diagrams to show the different types of fertilized eggs (and of individuals derived from them), when the two types of ova shown in figure 27 are fertilized by the two usual types of sperm. A, ovum containing two X's, fertilized by sperm containing Y, yields a female bearing in her cells two X's (both from the ovum) and a Y. B, ovum containing no X, fertilized by a sperm bearing X, yields a male bearing in its cells an X (derived from the sperm), but no Y. The X's of the ovum, shown in outline, are defective, producing white eyes in place of red. Hence the XXY females have white eyes, the X males normal red eyes.

produced (since but one X is present), and *these males have red eyes,* like the father, since their X comes from the father. Here then, contrary to the usual rule, the sons are like the fathers, the daughters like the mothers. The normal and defective characteristics follow precisely the distribution of the normal and defective X-chromosomes, whether these are distributed in the usual way, or abnormally.

In these cases, the abnormal distribution of the X-chromosomes is revealed by examination with the microscope. The exceptional white-eyed females have two X's and one Y (figure 28), while the usual red-eyed ones have two X's without a Y. The exceptional red-eyed males have but one X and no Y (figure 28), while the usual white-eyed ones have both an X and a Y. A race of fruit-flies was found by L. V. Morgan[3] and has been long cultivated, in which the two X's of the female regularly cling together and pass together into one ovum. This race therefore gives usually the exceptional results just described. In this race all details can be, and have been, fully studied with the microscope.

Such exceptional cases are obviously of the greatest importance and interest. They clearly demonstrate that the sex-linked characteristics of the individual depend upon particular X- chromosomes, however the latter are distributed. *The rules of distribution of the characteristics are the rules of distribution of the chromosomes*—whether the latter are normal or exceptional. To change the distribution of the characteristics —to change the "rules of inheritance"—it is necessary only to change the distribution of the chromosomes, as the race found by L. V. Morgan shows.

It is clear then that different X-chromosomes have different peculiarities, giving rise to different inherited characteristics, each of which follows the distribution of its X. More than 50 of these different sex-linked characteristics are known in the fruit-fly alone; so that more than 50 different types of X-chromosomes are known in that insect. In man a considerable number of different types of X-chromosomes are known, each giving rise to a different "sex-linked" characteristic.

Several Characteristics Following a Particular Chromosome

Here arises a question of the greatest interest. May two or more of these characteristics result from the same single X-chromosome?

Examination shows that they may. In the fruit-fly, one type of X-chromosome causes the production of a body that has a yellow color, another the production of white eyes. But the same individual may have both yellow body and white eyes, and this may occur even in a male, which has but one of the X-chromosomes. Moreover, when such a male produces offspring, both these characteristics follow the distribution of the father's X-chromosome, in the way already described.

More than two characteristics can thus follow the distribution of one X-chromosome. Four, five, six, or more sex-linked peculiarities may be present in one male, and follow the distribution of his single X-chromosome; cases of this sort have been thoroughly studied. Each of these same peculiarities may in other cases be connected with a different X-chromosome.

Is the Chromosome Composed of Diverse Parts?

Here emerges one of the fundamental questions of the science of genetics. When two or more characteristics follow a single X-chromosome, has this chromosome two or more parts corresponding to the different characteristics? Or is such a chromosome an inseparable unit, so constituted as to cause the production of several peculiarities?

This question is clearly answered by observing the results of experimental breeding. *Two or more characteristics that are following the same single X-chromosome may become separated so as later to follow different X-chromosomes.* They therefore result from peculiarities of different separable parts of the chromosome. This fact is so important that a typical case should be followed through in detail, in order that the nature of the evidence may be seen.

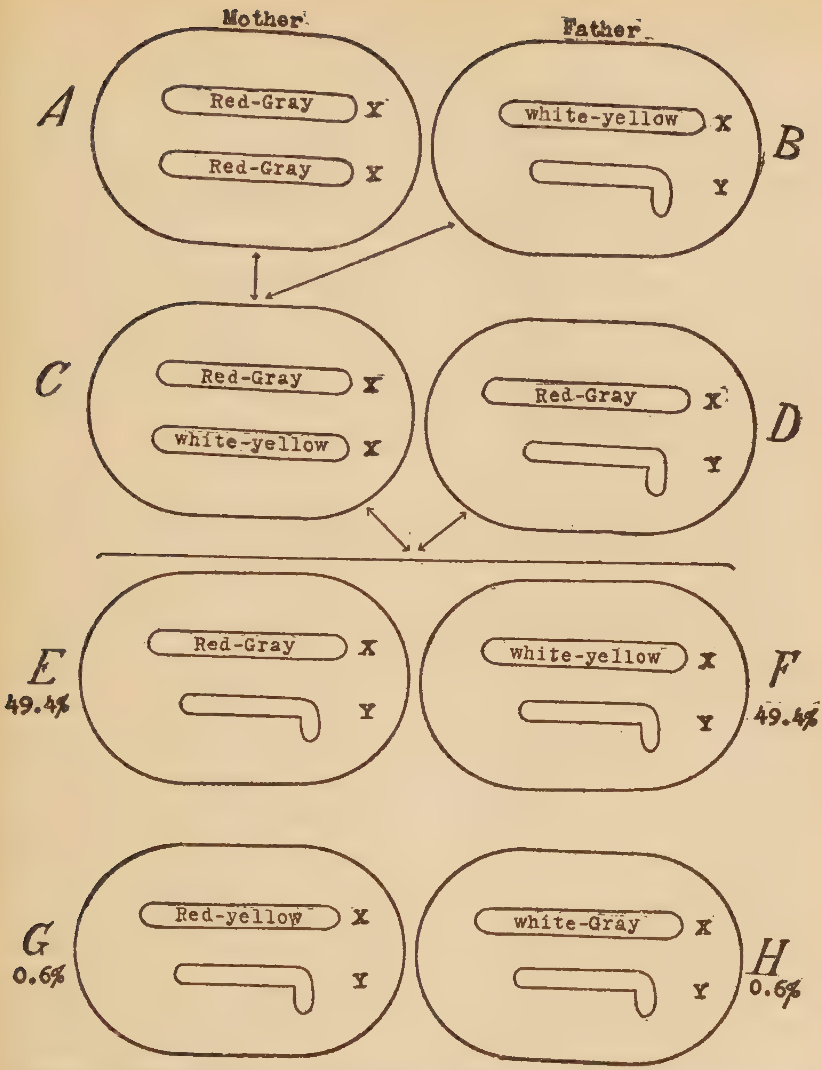

Mother
Father
A
Red-Gray
X
Red-Gray
X
white-yellow
X
Y
B
C
Red-Gray
X
white-yellow
X
Red-Gray
X
Y
D
E
49.4%
Red-Gray
X
Y
white-yellow
X
Y
F
49.4%
G
0.6%
Red-yellow
X
Y
white-Gray
X
Y
H
0.6%

Figure 29—Diagram of results of breeding that prove the X-chromosome to consist of separable parts having different effects on development. A female *A*, whose X-chromosomes yield red eyes and gray body, is mated with a male B whose single X-chromosome yields white eyes and yellow body. Their daughters C have together in the same cell the two kinds of chromosomes, one yielding red and gray, the other yielding white and yellow. In a few of the cells of such daughters these chromosomes exchange parts, so that one now produces red eyes and yellow body, the other white eyes and gray body. This is demonstrated by the fact that such daughters produce a small number of sons (G and H) whose single X-chromosomes produce these new combinations; along with many sons (E and F) in which the single X-chromosomes produce the original combinations of characteristics.

A male fruit-fly is selected that has white eyes and yellow body (B, figure 29). These are recessive sex-linked characteristics, and both are connected with the single X-chromosome of the male. Such a male is mated with a female whose two X-chromosomes are normal, so that she has normal red eyes and gray body (A, figure 29). Their daughters (C, figure 29), according to the usual rule, get one normal ("red-gray") X-chromosome from the mother, one "white-yellow" X-chromosome from the father. In their cells therefore these two kinds of X-chromosomes are present side by side in the same cell (C, figure 29). Here, as the results show, *the two kinds of chromosomes may exchange parts,* so as to form a new combination of the characteristics.

This is discovered as follows: Let some of these daughters, C, with the two types of X-chromosomes, be mated with normal males (D, figure 29), having normal X-chromosomes, and therefore red eyes and gray body. We need to observe only the sons that they produce (see figure 29, E, F, G, H). Sons, as we know, get their single X-chromosome from their mother only. The two kinds of X-chromosomes in these mothers (C, figure 29), as we know, become separated, passing into different ova. The ova with normal or "red-gray" chromosomes, when fertilized by a sperm containing a Y from the male, of course produce sons with red eyes and gray bodies (figure 29, E). The ova with recessive or "white-yellow" chromosomes (from the original male), produce sons with white eyes and yellow body (F, figure 29). Most of the sons produced are of these two types. But in addition to these *there are a few sons* (about one per cent of all) *that have a new combination of characteristics*. There are some sons that have red eyes and yellow body (G, figure 29), and an equal number that have white eyes and gray body (H, figure 29). These new combinations continue in later generations to follow particular X-chromosomes.

So it is clear that the diverse X-chromosomes that were present together in the cells of the mothers of these sons have in some cases exchanged parts, so as to make chromosomes with new combinations of peculiarities. This answers the question as to whether each chromosome is an inseparable unit, or is composed of parts. Clearly, the white eye and the yellow body of the original grandfather were due to diverse parts of his single chromosome, for these parts have now become separated, and one has combined with a part of the X-chromosome derived from the original grandmother. And the red eye and gray body of the grandmother too were due to diverse parts of her X-chromosomes, for these parts have now separated and combined with a part of the "white-yellow" chromosome. This exchanging of parts of chromosomes is known as "crossing over"; it has been found to occur on a vast scale.

The single chromosome then, it is proved, is composed of separable parts, having diverse effects on development. This is one of the basic facts in our knowledge of heredity and development.

How many diverse parts has an X-chromosome? By an immense number of experiments of the kind just described, it can be shown that any of the 50 or more different sex-linked characteristics of the fruit-fly can be brought together into one X-chromosome, and later separated again into different ones. It follows therefore that an X-chromosome of the fruit-fly has 50 or more separable parts. There is no escape from this conclusion. An X-chromosome is proved to be a compound structure, consisting of many diverse and separable parts, each affecting the development of the organism, and therefore its characteristics, in a different way.

It is convenient to have a name for these parts, and, as we know, they are commonly called genes. The word "gene" means nothing but these separable parts, having diverse effects on development, of which chromosomes have been proved to consist. In this sense therefore genes are demonstrated realities; not "hypothetical units" with mystic properties, as those unfamiliar with the evidence have imagined.

The known number of diverse parts, or genes, contained in the X-chromosome of the fruit-fly is continually increased as investigation continues. At the present time over 50 are positively known; beyond doubt the chromosome contains a hundred or more. In other organisms the X-chromosome has been relatively little studied; but as adequate study is made, these, too, are found to contain many diversely acting parts or genes.

Other Chromosomes

By the use of methods similar to those described above for the X-chromosome, though requiring more complex breeding experiments, it has been shown that each of the other chromosomes is likewise composed of a large number of diverse parts (genes), separable through "crossing over," and each with its characteristic effect on development. This has been as fully demonstrated for the other chromosomes as it has for the X-chromosome. In the fruit-fly a large number of diverse parts (approaching one hundred) have been found in each of the other two large chromosome pairs—those labeled II and III in figure 17. In the small chromosome IV (figure 17), only a few such separable genes have been found. Only the Y-chromosome shows little indication of the existence of separable parts, separate genes. The Y-chromosome appears to have little effect on development; it seems to be a degenerate chromosome. Yet, as set forth in later paragraphs, in some organisms different Y-chromosomes have been found to produce diverse development in respect to a few characteristics.

The other chromosomes are distributed to the offspring in a way differing greatly from the course followed by the X-chromosomes. To distinguish them from X and Y, they are commonly called *autosomes*. While, for example, any male has but a single X, it always has two members of any pair of autosomes. The X from a male parent, as we saw, passes only to his daughters; but either member of any pair of autosomes may pass either to a son or to a daughter.

In consequence of this different method of distribution, any characteristics due to peculiarities of a particular autosome show rules of inheritance differing much from those dependent on particular X-chromosomes. The characteristics result-

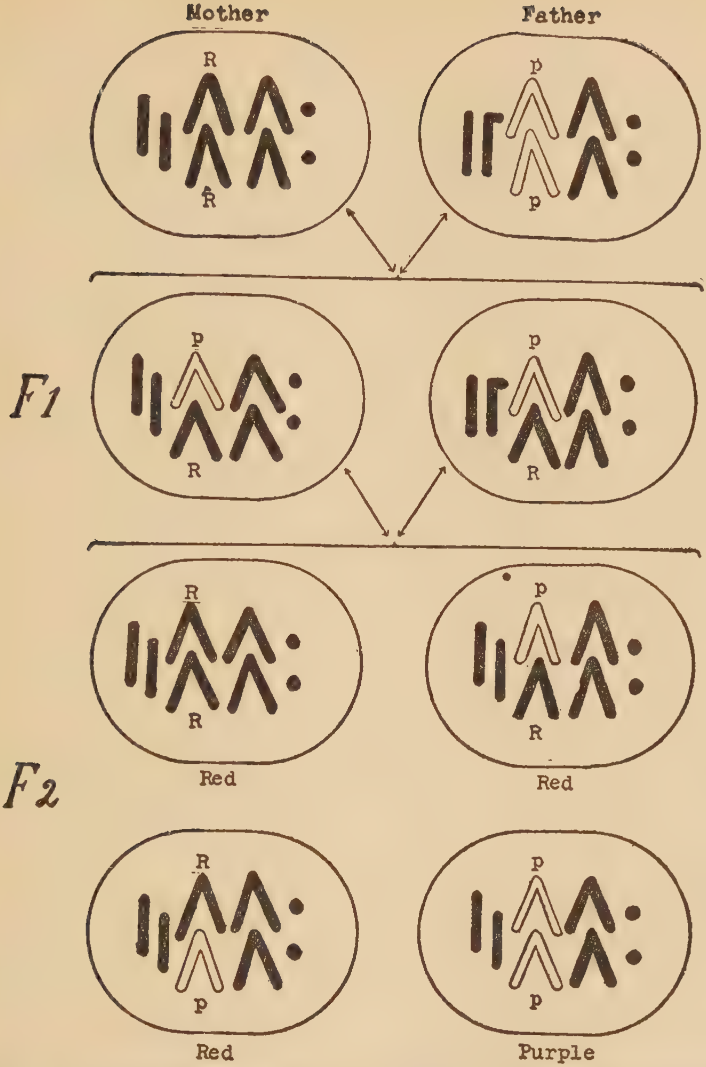


Figure 30—Diagram representing the course of inheritance (typical Mendelian), in cases in which the difference between a dominant and a recessive characteristic is due to a difference in an autosome of the two parents. The father has the two members of his second pair of chromosomes (represented in outline) so modified as to yield the recessive eye color purple (p); while in the mother the second pair is unmodified and so yield the usual red (R) eye color. Each of the offspring (F1) contains one of the modified autosomes (p), one unmodified (R); hence each has red eyes. When two such offspring are mated together, they yield in F2 the combinations RR, pR, Rp and pp; that is, the Mendelian ratio of 3 reds to one purple.

ing from peculiarities in autosomes show typical Mendelian inheritance, as contrasted with the sex-linked inheritance of those due to peculiarities in X. This is illustrated in figure 30, showing a typical case in the fruit-fly. The father's autosomes of pair II are so modified that they cause him to have purple eyes (p) instead of the usual red eyes (R). The mother's autosomes of that pair (R) being of the usual type, she has red eyes. The offspring (F1) of these two receive one of these normal autosomes from the mother, one of the modified ones from the father. It turns out that the normal autosome is dominant over the modified one, so that these offspring all have red eyes, though each contains one of the modified chromosomes (p) from the father. When now two of these children are mated together, most characteristic and interesting results appear. Each such parent of course produces two types of germ cells, one containing the unmodified chromosome R, the other the modified chromosome p. In the mating, each type of germ cell (R and p) of the father unites with each type (R and p) of the mother. So, placing the designation of the father's germ cells first, the result is the following four combinations: RR, Rp, pR, pp. The first three of these give rise to individuals with red eyes, since R is dominant over p; the last one gives rise to individuals with purple eyes. Thus arises the typical "Mendelian ratio," of three dominants to one recessive. This typical Mendelian inheritance, with proportions of three individuals of one type to one of another, is shown by all characteristics resulting from the peculiarities of autosomes (except in cases where neither characteristic is entirely dominant). And wherever this typical Mendelian inheritance occurs, it follows that the characteristic so inherited depends upon a peculiarity of some autosome.

The Laws of Inheritance are the Rules of Distribution of the Parts of the Chromosomes

These facts illustrate the general principle that *the "laws of inheritance" are essentially the rules of distribution of the* *chromosomes,* taken in connection with the facts of dominance and recessiveness. A characteristic due to a peculiarity of X follows one law of inheritance; a characteristic due to a peculiarity of an autosome follows another. If through an accident the X-chromosome is distributed in an unusual way, the characteristic shows the same unusual distribution. The same is true of the autosomes. In the fruit-fly the small fourth chromosome (IV, figure 17) is sometimes irregularly distributed; and the characteristics dependent on it then follow its irregular distribution (Bridges [4]).

As the Y-chromosome is distributed differently from either the X-chromosome or the autosomes, any characteristics dependent on peculiarities of particular Y-chromosomes shows still other laws of inheritance. A number of cases of this sort have of late become known. Such characteristics descend directly from father to son exclusively. They never appear in females, and are never transmitted through females. One case of this kind is known in the fruit-fly and a considerable number of such characteristics, dependent on peculiarities of the Y-chromosome, have been discovered in a certain fish.[5]

All these relations illustrate the fact that the special laws of inheritance are not the consequence of some general and universal property of living material; but on the contrary are the result of very special peculiarities of particular parts of particular organisms. Different characteristics show different laws of inheritance, because they depend on peculiarities of chromosomes that follow different methods of distribution. When the method of distribution of the chromosome is changed, the method of inheritance changes; as has been above illustrated. There are in higher organisms three main methods of inheritance; the sex-linked, depending on peculiarities of the X-chromosome; the typical Mendelian, depending on peculiarities of some autosome; and that shown by the few characteristics that depend on peculiarities of a Y-chromosome. By the use of X-rays, it has been possible in some cases to cause a portion of the X-chromosome to become attached to an autosome. Thereupon the characteristics that depend on that portion of the X-chromosome change from the sex-linked type of inheritance to the Mendelian type.

In certain organisms there are apparently still other methods of distribution of chromosomes; and correspondingly there are other rules of inheritance.[6] In the reproduction of many lower organisms, offspring arise from a single parent only; and receive all the chromosomes of the parent. In such reproduction there is neither Mendelian nor sex-linked inheritance, but a totally different type. The rules of inheritance are a faithful reflection of the methods of distribution of the chromosomes.

Given Characteristics Diversely Inherited in Different Matings

From the facts just stated, in connection with other facts as to the operation of chromosomes, arise certain relations that are of the greatest practical importance; relations that are very commonly neglected. As set forth on an earlier page, and more fully in Chapter VIII, any characteristic whatever is produced by the interaction of many genes; and it may be altered by a change in any one of these many genes. Some of these genes are in the X-chromosome, some in other chromosomes. If the characteristic becomes modified by a change in a gene that lies in the X-chromosome, in later generations that characteristic will be inherited according to the sex-linked method. But if it becomes modified by a change in a gene that lies in an autosome, that same characteristic will thereafter be inherited in the typical Mendelian method. The same characteristic will therefore show in some cases one type of inheritance; in other cases another type. This fact is of so great practical importance that a typical case should be followed:

In the fruit-fly the eye color is usually red; and this usual red color is produced by the coöperative action of fifty or more genes, some in the X-chromosome, some in the different autosomes. At times a gene in the X-chromosome is so modified as to cause the eye color to be white. If an individual with such white eyes is mated to one with red eyes, the two characteristics show in later generations sex-linked inheritance, as illustrated in figures 22 and 23. The white color shows recessive sex-linked inheritance, the red color dominant sex-linked inheritance.

In other individuals the red color of the eye is altered to purple by a change in a gene of one of the autosomes (II). If an individual with purple eyes is mated to one with red eyes, the two characteristics now show typical Mendelian inheritance (figure 30), the purple being recessive, the red dominant. Thus the dominant character red shows in this case typical Mendelian inheritance, while in the case described in the preceding paragraph it shows the very different sex-linked type of inheritance. *The type of inheritance that it shows depends upon the location, in the individual with which it is mated, of the gene that alters the red color.* The same red-eyed individual will yield sex-linked inheritance of red when mated with a white-eyed individual; typical Mendelian inheritance of red, when later mated with a purple-eyed individual.

This example is typical. Any dominant character will show the type of inheritance that is determined by the location of the corresponding recessive gene in the individual with which it is mated.

A recessive character, showing particular bodily manifestations, may likewise in diverse instances show different methods of inheritance. As set forth on page 17, in the fruit-fly a purplish eye color is induced by a modification of a gene ("purple") in the second autosome. When individuals with such purplish eyes are mated with others having red eyes, the purplish eyes are inherited in later generations as a typical Mendelian recessive characteristic. But in other cases the purplish eye color results from alteration of a gene ("garnet") in the X-chromosome. When such purplish-eyed individuals are mated with red-eyed individuals, the purplish color is inherited in later generations as a recessive sex-linked characteristic.

Thus the fact that a particular characteristic shows in given instances a particular type of inheritance does not make it certain that in other cases it will show that type. Color-blindness is said in some cases to show sex-linked inheritance. In other cases it might perfectly well show typical Mendelian inheritance. The type of inheritance shown depends upon what particular chromosome contains the genes in the two parents, that differ in such a way as to cause the given difference in characteristics; and this may be diverse in different cases. It is a common custom to speak of a particular characteristic as a "sex-linked character," or a "typical Mendelian character." But these designations express the situation only in the matings that the author has in mind. In other matings it may turn out that the same characteristic will show another type of inheritance.

Similar relations exist with respect to dominance and recessiveness. Whether a particular characteristic is dominant or recessive depends upon what characteristic it is mated with. Mated with bar-eyes, the normal eye structure of the fruit-fly is recessive; but mated with facet-eye (another abnormality) the normal eye structure is dominant. Dominance and recessiveness are relative; they depend on what comparisons are made.

Again, in some cases two parents that differ in a certain characteristic have but one differing gene that affects that characteristic; in other cases the parents differ in two or more such genes. The method of inheritance will differ in the two cases; the proportions of offspring showing the different characteristics depend on the number of genes in which the parents differ. If the dominant and recessive parents differ in but one gene-pair, the descendants in the second generation are in the proportion of three dominants to one recessive; if the parents differ in two gene-pairs, the second generation shows fifteen dominants to one recessive. The same characteristic will be inherited sometimes in one of these ways, sometimes in the other—depending on the relative genetic constitution of the two parents.

Thus the method of inheritance is a relative matter, depending on the relation of the genes in one parent to those in the other. It is not characteristics in themselves that are inherited in a particular way, but only the difference between the two characteristics in the different individuals that are mated. Discovery of how a certain characteristic is inherited in one set of cases does not show how it will be inherited in others. A characteristic that is dominant in one set of matings may be recessive in another; a characteristic that is sex-linked in one set of matings may be "typical Mendelian" in another; a characteristic that appears in the three-to-one ratio in a given set of matings may appear in quite different ratios in another set. The diversity between parent A and parent B may be due to a single gene difference lying in the X-chromosomes; the inheritance will then be of the sex-linked type. But the same outward diversity between A and another individual C may be due to a single gene difference lying in another chromosome; then if A and C are mated the inheritance will be of the Mendelian type. If the genes that differ were in the Y-chromosome, then inheritance would be of a still different type. Much confusion will be avoided if inheritance is understood to apply rather to differences between particular individuals than to characteristics taken in any absolute sense. The method of inheritance is relative to the matings that are made.

Linkage of Characteristics

As we have seen (page 58), many diverse characteristics are due to peculiarities of the different parts, or genes, of a particular chromosome. Any two or more of these characteristics may be connected with a particular single chromosome; a particular X-chromosome, for example. These then pass all together, with that chromosome, to such of the offspring as receive the latter. For this reason they are said to be "linked." This linkage is a most important phenomenon in inheritance. It is shown by the fact that if one of the grandparents has a combination of two or more characteristics resulting from genes lying in a single chromosome, then if in a grandchild one of the characteristics of this combination appears, usually all the others—the entire combination—appear also. The same combination of characteristics that passes to the parent from a grandparent is usually passed by the parent to the grandchild—provided those characteristics are due to genes of the same chromosome. In a small proportion of the children, however, a new combination is made, by "crossing over." Figure 29 illustrates these results of linkage.

All of the diverse characteristics that depend on the genes of a single chromosome—so that any of them may be linked together in the way just described—are said to constitute a "linkage group." In the fruit-fly there are fifty to a hundred characteristics that constitute the linkage group connected with the X-chromosome. The other chromosomes show a similar situation. Since genes may be exchanged by the two chromosomes of the same pair, all characteristics connected with either of the chromosomes of a pair are held to constitute a single linkage group. There is thus a linkage group for each pair of chromosomes; a set of characteristics that tend to be inherited together, so long as they are connected with the same chromosome of the pair. In any species the number of different linkage groups is discovered by breeding experiments, while the number of pairs of chromosomes is independently discovered by the use of the microscope. In organisms in which adequate study has been made, the two numbers are found to be the same. In the common fruit-fly, Drosophila melanogaster, there are four such linkage groups, connected with the four pairs of chromosomes. In another species (Drosophila virilis) there are six linkage groups and six pairs of chromosomes; in another (Drosophila obscura), five. In the garden pea and in the sweet pea there are eight pairs of chromosomes, and correspondingly eight of these groups of linked characters. In no case has the number of diverse linkage groups been found to exceed the number of pairs of chromosomes. In man, since there are 24 pairs of chromosomes, it will doubtless be found that there are 24 groups of linked characteristics; though it will certainly require many years of work to identify these.

Maps of the Genes

By extension and refinement of such breeding experiments as are described above it has become possible to discover, for some organisms, not only what characteristics are bound up with the genes of particular chromosomes, but how these genes are arranged in the chromosomes. At the period when the genes are exchanged from one chromosome to another, the chromosomes are linear thread-like bodies, with successive thickenings (figure 3, page 5). The genes are found to behave as if they were arranged in serial order on these threads. In the separation of the genes of the same chromosome at "crossing over," it is the genes that are farthest apart that become separated more frequently—as might be expected—since there is between them a longer distance, in any part of which the chromosome may break. On this basis, it has become possible, through hundreds of thousands of breeding experiments, to make maps of the chromosomes of the fruit-fly, Drosophila, showing the order in which the different genes are arranged in series (figure 31). The correctness, in essentials, of these maps is fully confirmed by further study. When "crossing over" or exchange occurs between two chromosomes of a pair, usually there is but a single break in each chromosome. In such cases, all the genes on one side of this break separate from all those that the map shows to be on the other side of this break; one of the sets becoming connected with a corresponding part of the other chromosome (as illustrated in figure 13, page 23). That is, the chromosomes do not exchange single genes, but exchange whole blocks of them, these being blocks of genes shown by the maps to be near together in successive order. Again, through the action of X-rays, or in other ways, at times a piece of one chromosome becomes broken off and attached to another chromosome, where it may be seen under the microscope (figure 32). Individuals in which this has occurred may be bred and multiplied. When this is done, a set of genes shown on the map to lie in serial order in the part of the chromosome that has been thus broken off and transferred, are found to

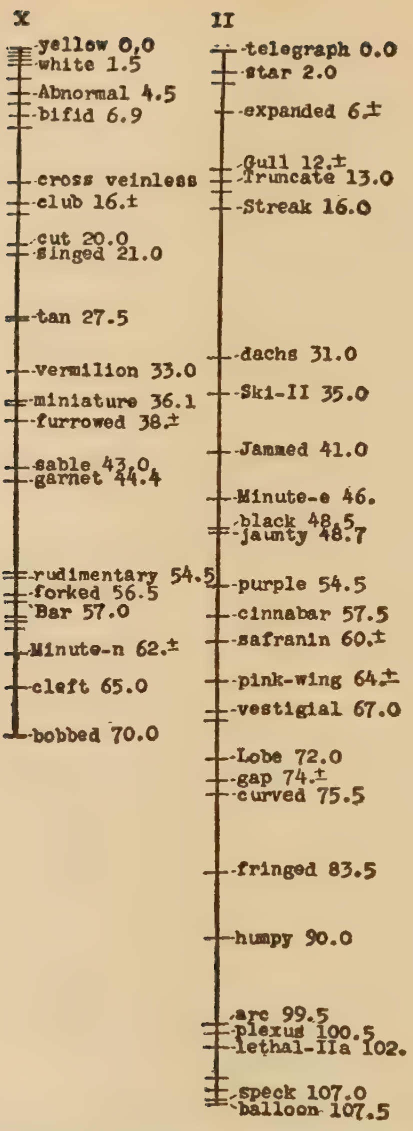

X
yellow 0,0
white 1.5
Abnormal 4.5
bifid 6.9
cross veinless
club 16.±
cut 20.0
singed 21.0
tan 27.5
vermilion 33.0
miniature 36.1
furrowed 38.±
sable 43.0
garnet 44.4
rudimentary 54.5
forked 56.5
Bar 57.0
Minute-n 62.±
cleft 65.0
bobbed 70.0
II
telegraph 0.0
star 2.0
expanded 6.±
Gull 12.±
Truncate 13.0
Streak 16.0
dachs 31.0
Ski-II 35.0
Jammed 41.0
Minute-e 46.
black 48.5
jaunty 48.7
purple 54.5
cinnabar 57.5
safranin 60.±
pink-wing 64.±
vestigial 67.0
Lobe 72.0
gap 74.±
curved 75.5
fringed 83.5
humpy 90.0
arc 99.5
plexus 100.5
lethal-IIa 102.
speck 107.0
balloon 107.5

Figure 31—Map of the X-chromosome, and of chromosome II of Drosophila, showing the relative serial positions of the genes. Based on the maps given by Morgan, Bridges and Sturtevant, The Genetics of Drosophila, page 92. Names are here given for only a limited number of the genes that have been located.

be "linked" in inheritance with the genes of the chromosome to which the piece has become transferred. In every way that the matter has been tested, the linear order of the genes, and the essential correctness of the maps of the chromosomes based on that order, have been confirmed. In the early days of investigation there was fierce criticism of this conception; but such criticism has now practically disappeared. Anyone who examines in detail the vast body of evidence collected on this point is forced to accept the linear order of the genes, in the way shown on the maps. The reader may therefore look upon this as established; and may accept with confidence the relations between genes, and between characteristics, that it displays. These relations are fundamental for many of the problems of heredity and of individuality; as is illustrated in chapter I. Anyone who neglects them is certain to go wrong in his deductions and generalizations.

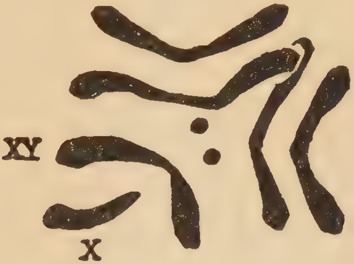


Figure 32—Cell of a Drosophila in which a portion of the Y-chromosome has become attached to the end of one of the X-chromosomes (at XY). A gene in Y is in these cases linked in inheritance with genes lying in the X-chromosome; though normally genes in these two chromosomes always pass into different individuals. After Stern.

Summary

In sum, positive and inescapable experimental evidence proves that the chromosome is a structure composed of many diverse parts, each part or gene having a definite effect on development, and therefore a definite effect on the characteristics of the individual produced. The rules of inheritance of characteristics result from the way these chromosomal parts are distributed in passing through the germ cells from parent to offspring. To understand inheritance and development it is essential to understand the behavior and distribution of these chromosomal parts.

NOTES AND REFERENCES ON CHAPTER II

For details of the evidence set forth in chapter II, see especially the publications of Morgan, Bridges and Sturtevant, on Drosophila. Among these may be mentioned particularly: *Sex-linked Inheritance in Drosophila,* by T. H. Morgan and C. B. Bridges (Carnegie Institution Publication No. 237, 1916); *Contributions to the Genetics of Drosophila melanogaster,* by T. H. Morgan, C. B. Bridges, and A. H. Sturtevant (Carnegie Institution Publication No. 278, 1919); *The Third Chromosome Group of Mutant Characters of Drosophila melanogaster,* by C. B. Bridges and T. H. Morgan (Carnegie Institution Publication No. 327, 1923); *The Genetics of Drosophila,* by T. H. Morgan, C. B. Bridges, and A. H. Sturtevant, in Bibliographia Genetica, Vol. 2, 1925, pp. 1–262; *The Theory of the Gene,* by T. H. Morgan (New Haven, Conn., 1926).

1. Page 38. K. Belar gives photographs showing plainly the chromosomes in living cells (*Über die Naturtreue des fixierten Präparats.* Proceedings of the Fifth International Congress of Genetics, in Supplementband, 1928, to the Zeitschrift für Induktive Abstammungs-und Vererbungslehre, pp. 403–405.)

2. Page 56. See C. B. Bridges, *Non-disjunction as Proof of the Chromosome Theory of Heredity.* Genetics, Vol. 1, 1916, pp. 107–163.

3. Page 57. See L. V. Morgan, *Non-crisscross Inheritance in Drosophila melanogaster.* Biological Bulletin, Vol. 42, 1922, pp. 267–274.

4. Page 65. See C. B. Bridges, *Genetical and Cytological Proof of Non-disjunction of the Fourth Chromosome of Drosophila melanogaster.* Proceedings of the National Academy of Sciences, Vol. 7, 1921, pp. 186–192.

5. Page 65. For inheritance of characteristics that follow the Y-chromosome, the following papers may be consulted: C. Stern, *Vererbung im Y-Ghromosom von Drosophila melanogaster,* Biologisches Zentralblatt, Vol. 46, 1926, pp. 344–348; also, O. Winge, *The Location of Eighteen Genes in Lebistes reticulatus,* Journal of Genetics, Vol. 8, 1927, pp. 1–43.

6. Page 66. For still other methods of distribution of inherited characteristics, see C. W. Metz, *Chromosome Behavior and Genetic Behavior in Sciara (Diptera)*. II. Genetic Evidence of Selective Segregation in Sciara coprophila. Zeitschrift für Induktive Abstammungslehre, etc. Vol. 45, 1927, pp. 184–200.

III

HOW DO THE GENES ACT IN PRODUCING THE INDIVIDUAL? THE NATURE OF DEVELOPMENT

At the beginning any individual of man or other organism is a single cell, containing the many diverse genes in two sets derived from the two parents; these imbedded in a mass of protoplasm—the *cytoplasm* of the egg (see figure 33, A at *c*). This minute cell divides; the number of cells increases; the form and structure change. A vast transformation occurs, through a slow process of development. The relatively simple cell becomes a complex structure, with a great number of diverse parts. The complete individual results, with his many different organs, his many different functions and activities.[1]

We know that the way this process of development takes place is greatly affected by the genes, since different sets of genes give different development, resulting in diverse individuals. How, then, do the genes operate in development? What is the nature of the developmental process?

Interaction of Genes and Cytoplasm

As development is studied, it is found that another part of the cell, aside from the genes, plays a great role; though a role differing much from that of the genes. This is the cytoplasm, the mass of protoplasm forming the main bulk of the egg (figure 33, *c*). In this mass is imbedded the capsule or nucleus that contains (or is composed of) the genes (figure 33, *n*). The cytoplasm is a most complex mass, but it appears not to contain separable substances, acting as unit particles that may be transferred, singly or in groups, from one cell to another, as is true of the genes of the nucleus. The different

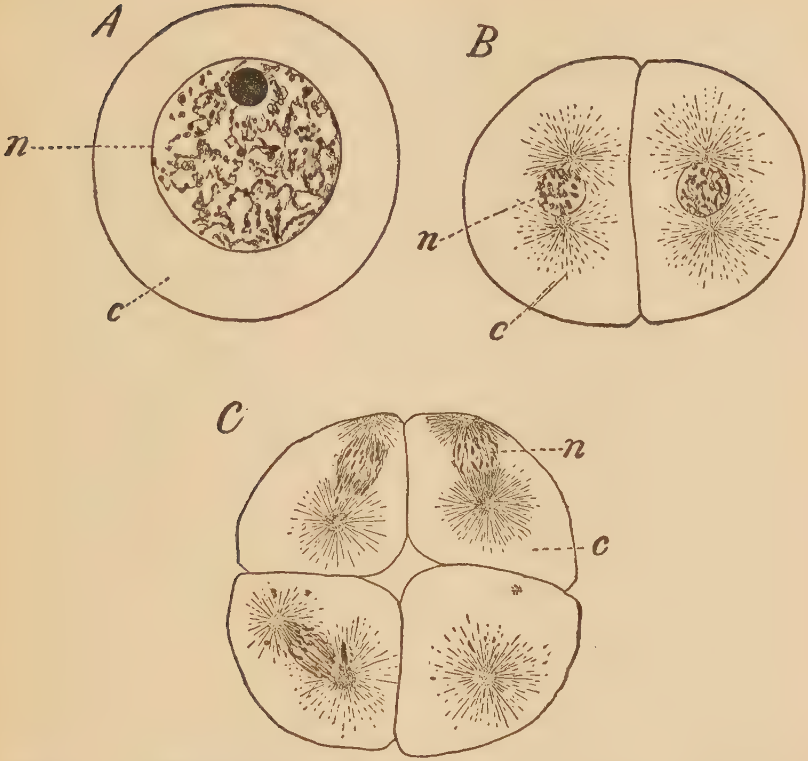


Figure 33—Individuals in earliest stages of development. A, ovum of the starfish, before fertilization and before division. B, after division into two cells; C after division into several cells. *n*, nuclei, showing (particularly in B and C) the small dark chromosomes, in which are the genes. In A the nucleus is greatly enlarged. c, cytoplasm or cell body. Based on the photographs in Wilson's Atlas of Fertilization and Karyokinesis of the Ovum. (Columbia University Press, 1895.)

individuals of the species, though differing greatly in their genes, all have at the beginning the same, or nearly the same, type of cytoplasm. Thus later differences among the developed individuals are as a rule not due to early differences in their cytoplasm, as they are to early differences in their genes. This is the ground for calling the genes, rather than the cytoplasm, the "material basis of heredity." Though the cytoplasm is of the greatest possible importance in development, the original basis for diversity of hereditary characters lies, not in it, but in the genes. Only in certain plants are cases known in which different individuals begin with different types of cytoplasm (with respect to the presence or absence of color-producing bodies), yielding diverse characteristics.

The cytoplasm of the fertilized egg comes almost entirely from the mother. The sperm bears a minute quantity of it, most of which is left outside when the sperm unites with the ovum. However, a minute bit of this sperm cytoplasm enters along with the genes from the father, and plays an important role in aiding to start development.

The cytoplasm is the medium in which the genes live and operate. It is modified, transformed, by the action of the genes, so that at later stages of development the cytoplasm differs greatly from that which was present in earlier stages. This changed cytoplasm reacts anew with the genes, causing these now to change their action, resulting again in new cytoplasmic products. This continues until ultimately the diverse tissues and organs of the adult body have been produced, as a result of the changes in the cytoplasm. Thus the different parts of the body finally differ, not in the genes that they contain (as a rule) but in the diverse constitution of the cytoplasm of their cells. The cytoplasm is the material out of which the parts of the diversified body are manufactured, through interaction with the genes. But in development the cytoplasm is not passive; it reacts upon the genes, and what the genes do, what they produce, is largely determined by the nature of the cytoplasm in which, at different stages of development, they find themselves.

Earliest Developmental Processes: Ground Plan of the Body Laid Down in the Cytoplasm of a Single Cell

The interaction of the genes and cytoplasm, that constitutes the fundamental process in development, begins in the egg before it has left the body of the mother; at this time it may be called the *ovum*. Important steps in the development of the individual are taken at this time, before the union of the ovum with the sperm. The ground plan of the body is then laid down, at least in some organisms; and the processes that occur in bringing this about are typical of the nature of development.

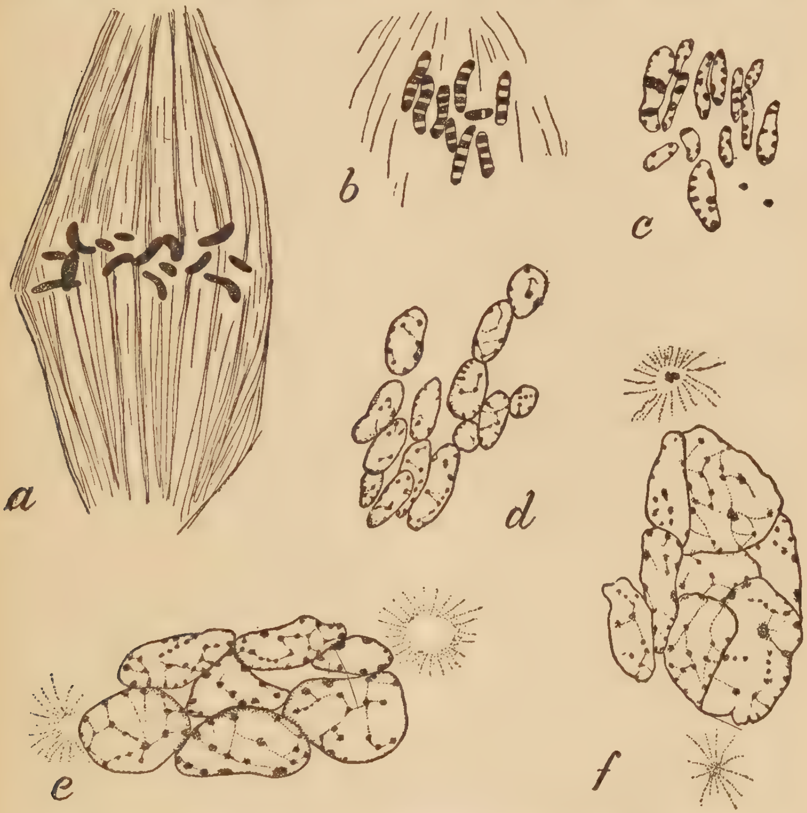


Figure 34.—Transformation of the condensed chromosomes (a) by absorption of fluid into vesicles which slowly enlarge (b, c, d, e, f), finally constituting the nucleus. The figures show the process in the cells of the egg of a fish, Fundulus. a to f, successive stages. After Richards (1917).

The cells that will give rise to the ova at first do not differ greatly from other cells in the body of the mother. Such cells divide many times. At a certain time one of these minute cells enters upon the developmental processes that finally result in an individual.

Such a cell immediately after the division that produced it (constituting in a sense the very earliest stage of an individual) has its genes gathered into minute condensed chromosomes (like those in figures 4, 15, 16); these are imbedded in the small mass of cytoplasm. The action of separate genes cannot be observed; but the behavior of the entire group of genes can be followed, since it is these that constitute the visible chromosomes. These chromosomes are seen to increase in size, to swell, by taking in material from the cytoplasm. This process is illustrated in figure 34. Each chromosome becomes a small vesicle (figure 34, a, b, c, d). These vesicles increase in size, until their boundaries touch, and they become crowded together (figure 34, e, f). They partially fuse, forming what is called the *nucleus*. In the main the nucleus is constituted by the partly united chromosomes; and the chromosomes in turn are constituted by the genes. Thus as we follow the activities of the nucleus, we are observing in the gross the action of the genes. These, as we have just seen, have taken in a large amount of material from the cytoplasm. Later it will be seen that they give off this material to the cytoplasm again. There is evidence that in the interval they have acted on this cytoplasmic material, have altered it; and when they give it off again, it is new material which goes to build up the developing body. This process of taking in cytoplasmic material and giving it off again, takes place at every cell division. It appears to be largely in this way that parts of the cytoplasm are chemically and physically changed; so that this is one of the fundamental processes in development.

In the single cell which is to produce an ovum, and so later an individual, another action of the gene-group, or nucleus, has been observed. It gives off into the cytoplasm droplets or particles of some substance which is visible through a special color reaction that it yields with certain dyes. This substance diffuses through the cytoplasm, and as this takes place the cytoplasm begins to increase greatly in volume; the cell grows. It becomes much larger than an ordinary cell, and takes on the characteristic appearance of an ovum (figure 33, A).

The gene-group or nucleus of this cell continues to enlarge by taking in additional fluid from the cytoplasm—doubtless modifying this material. It becomes a very large sac, the "germinal vesicle" (figure 33, A, *n*). Now occurs a striking process: the membrane surrounding this germinal vesicle dissolves, and the fluid that it contains passes out and mingles with the cytoplasm. The cytoplasm therefore now contains a large quantity of material that has been elaborated by the genes, within the nucleus. It is fully prepared for the first conspicuous step in the production of the new individual. This step is taken shortly after the nuclear substance has been poured into the cytoplasm. In certain animals in which the cytoplasm carries coloring matter, this first step is clearly seen. The entire interior of the ovum is observed to transform, to rearrange itself, to take on a definite structure. In a certain kind of sea urchin, having reddish droplets scattered throughout the ovum, the cytoplasm is seen to arrange itself in three zones (figure 35). Forming a middle zone is a broad band, in which most of the reddish pigment concentrates itself (figure 35, B, at r). Above this (in that part of the ovum by which the cell was originally attached in the mother's body) is a large zone of grayish material (g). And below the red zone is a smaller zone of rather clear material (c). *These three zones form the foundation plan for the new individual;* they are the first visible diversities produced in development. The large gray zone is what later produces the outer body covering and the sense organ of the young sea urchin; the red middle zone produces the lining of the primitive alimentary canal; and the clear lower zone produces the skeleton and other parts lying between the inner and outer layers of the young sea urchin's body. If one of these zones of material is removed or disarranged, there is a corresponding lack, or abnormality, in the developed parts of the later individual. The single cell

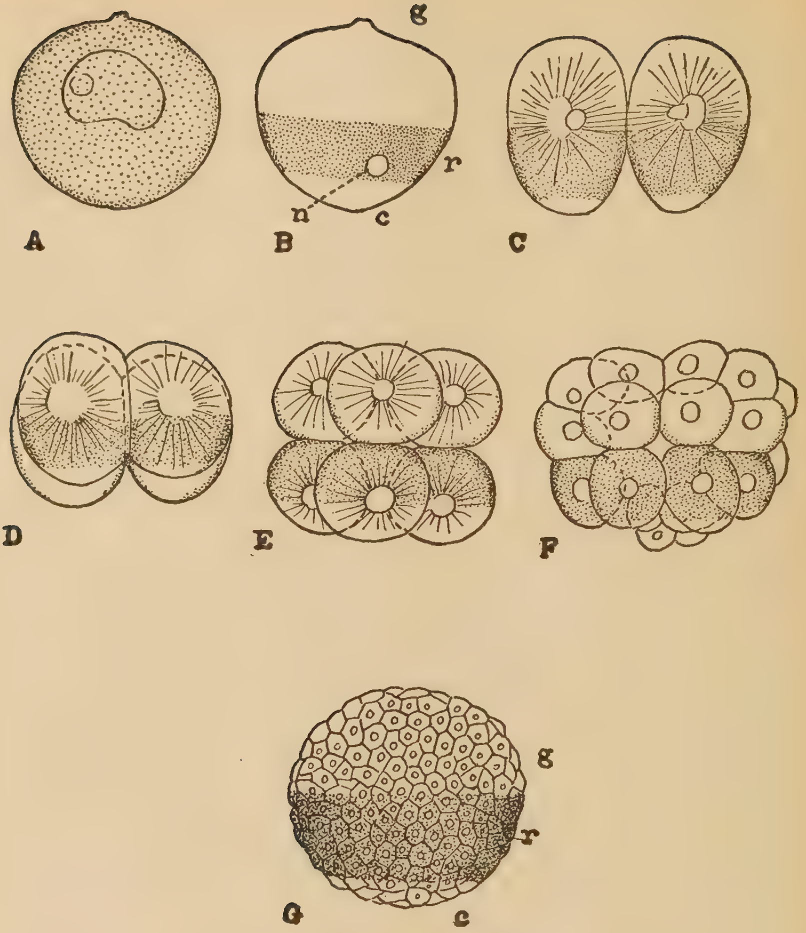


Figure 35—Successive stages (A to G) in the early development of a sea urchin, showing how the ground plan of the individual is laid down within the single cell. A, individual in the single-cell stage, before the bursting of the large germinal vesicle or nucleus—the red granules (represented by dots) scattered throughout the cytoplasm. B, later single-cell stage; the nucleus has discharged its fluid into the cytoplasm, and is now minute. The red granules have gathered into a zone (r), below the middle of the cell body. The body is therefore divided into an upper gray zone (g), an intermediate reddish zone (r), and a lower clear zone (c). C, two-cell stage; D, four-cell stage; E, eight-cell stage: F and G, later stages. Through all these stages the three zones can be traced. n, nucleus; g, gray zone; r, red zone; c, clear zone. Redrawn from the figures of Boveri (1901).

is in truth now an individual, with diverse parts that continue into its later life. These things were first observed by Theodor Boveri.

A similar process has been fully observed by E. G. Conklin in an animal not related to the sea urchin; one of the ascidians that has colored cytoplasm. After the germinal vesicle pours its fluid into the cytoplasm flowing movements occur, and, as in the sea urchin, the body of the cell becomes stratified into layers, but in a different pattern from that of the sea urchin. Three diverse layers are clearly distinguishable, and with careful study it is seen that two of these are subdivided, so that in all five zones can be seen. Each of these produces some definite structure or tissue of the later animal; together they form the ground plan for the later individual.

The details of these early developmental processes differ greatly in different animals, in correspondence with the fact that diverse results are produced in each. In some, processes of this sort occur early in development, giving rise to egg structures or "patterns" similar to those of the sea urchin and ascidian, but differing in details. In others, the corresponding changes do not occur till late, after the egg has divided into many cells. But in the nature of the fundamental processes, what occurs in the sea urchin and ascidian is typical; it gives the key to the nature of the main developmental processes. The individuals at this stage, before the egg has divided, are therefore worthy of careful examination.

Each individual is as yet but a single cell, containing all the chromosomes, all the genes. Yet parts of its body have become diverse; the body is differentiated into distinguishable portions, with important diverse functions (figure 35, B). The diverse parts are composed of cytoplasm; it is in the cytoplasm that developmental changes are occurring. This production of diverse cytoplasmic parts will be continued along with growth and division into cells, giving rise to the diverse tissues and organs of the developed body.

Ground Plan Laid Down under Influence of Mother's Genes Exclusively.

These first developmental changes in the cytoplasm, just described, take place under the influence of the genes. For it is the genes that constitute the chromosomes, and the chromosomes together constitute the nucleus, mainly or entirely. And it is the nucleus that gives off the fluid which mingles with and constitutes part of the cytoplasm, before the separation of the cytoplasm into diverse parts. Up to this point fertilization has not occurred, so that the chromosomes of the father are not present. Thus it is clear that *all the development thus far has taken place under the influence of the mother's genes only.* As this development has laid down the ground plan on which the new individual is constructed, *this ground plan of the body is due to the mother alone.* She has supplied all the cytoplasm and all the genes that are as yet present. The father, the producer of the sperm which is soon to fertilize this egg, plays no role in producing this ground plan of the new individual. Yet it is to be recalled that the mother's genes have come half from the male parent of the previous generation. Thus the male is not excluded from influence on these first steps in the development of the new individual; but it is the male of the preceding generation that exercises this influence, the maternal grandfather of the new individual, in place of its father.

Introduction of Genes from the Father

Now occurs quickly the loss of half the genes from the mother—the loss of one gene from each of the pairs present in the ovum—and their replacement by corresponding genes from the father. These processes are known as reduction and fertilization. Before these occur, the nucleus has poured its contained fluid into the cytoplasm, as already described. After this it is found that there remains of the nucleus a reserved portion of each chromosome, and therefore of each gene.

These reserved chromosomes are now minute separate bodies, with the genes in the closely packed condition. The chromosomes and genes up to this time are present in the usual pairs. They surround themselves with a membrane, forming a small nucleus, and this now divides twice, in such a way as to get rid of one member of each of its pairs of chromosomes, and so of one member of each of its gene pairs (figure 36). The rejected parts pass to the outside, as two small cells known as the polar bodies (figure 36 p). About this time the sperm has entered the egg, bringing with it one member of each of the chromosomes, of each of the gene pairs, from the male. These now range themselves with the remaining genes of the ovum, so that the genes and chromosomes of the new individual are again in pairs—one member of each pair from the mother, one from the father (see figures 18 and 19, pages 42 and 43). The rest of the developmental processes therefore take place under the influence of the genes from both parents.

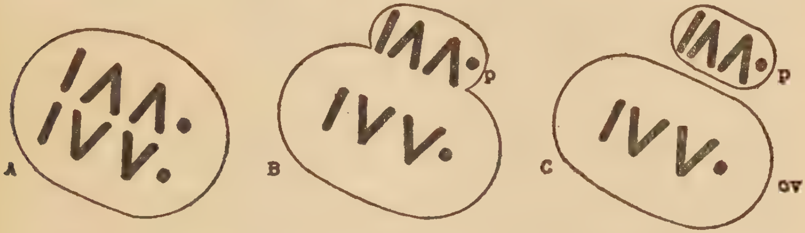


Figure 36—Diagram of the process of rejection from the egg of one member of each pair of chromosomes, and so of one member of each pair of genes. The original cell A contains four pairs of chromosomes. In B and C, one member of each pair is given off into the small polar cell (p), leaving the ovum (ov) with one member of each pair.

Cell Division, with Accompanying Developmental Processes

Now begins the division of the single cell into many cells. Certain details as to the first step in this process are of importance for the light they throw on the nature of development. In the single cell, the chromosomes (and genes) from father and mother have become grouped into a single nucleus. This nucleus divide; each of its component chromosomes divides; each gene of the chromosomes divides. The entire cell divides, and half of each nucleus, half of each chromosome, half of each gene, passes into each of the two cells produced. Each of the two cells therefore has the full set of paired genes.

It is found, on tracing the development further, that each of these two cells of which the individual now consists gives rise to half the later individual. In many animals, one gives rise to the right half of the body, the other to the left half; this is usually the case, for example, in the starfish (figure 33), the sea urchin (figure 35), and the ascidian.

A Fundamental Question of Development: Its Answer

Here emerges one of the fundamental questions of development. Why do certain cells give rise to one portion of the body, others to another portion? Is it because there are genes for different parts of the body, for particular tissues and organs, and because these genes become separated into the different cells? In this two-cell stage, does one cell contain materials only for the right half of the body, the other only for the left half?

This question is answered by separating the two cells and allowing them to develop thus isolated. This can readily be done in such animals as the sea urchin. And now each cell produces an entire individual. The cell that would have produced only the right half of the body now produces the left half as well; produces the entire body. Clearly, what each cell produces, at this stage, depends on its relation to the other cell, not upon different gene content. It is clear that both the cells contain a complete set of genes, since each can produce the entire animal.

This result turns out to be typical. As development occurs, at each cell division every chromosome divides, every gene divides, and every cell gets the entire set. There are apparently certain exceptions to this, notably in the nematode worms, but for most cells of most organisms it is true. Every one of the millions of cells of the adult body contains the complete set of paired genes.

But why then does each of the first two cells, when they are in contact, produce only half an individual, though each contains the genes for the whole? When the two cells are in contact, each has a different environment from that which it has when the two are separated. In the latter case, in the sea urchin egg, the entire surface of each cell is in contact with the sea water; in the former case a large part of the surface is in contact with another cell, and is shut off from the sea water. This is bound to make a difference in the respiration of the cell, in its taking in of oxygen and giving off of carbon dioxide; and other chemical processes must be affected. In some animals this is seen to make an immediate difference in the course of development. In certain starfish, the two cells when in contact have on their outer surfaces a cortical layer of protoplasm of different appearance from that which is within. Their inner surfaces, that are in contact, almost lack this cortical layer. But when the two cells are artificially separated, they become rounded, and the cortical layer gradually covers equally the entire surface. And now the two cells begin to develop each like an entire egg, instead of like a half egg. In some other organisms, the change from development like a half egg to development like a whole egg takes place more slowly; this is true in the sea urchin.

In such organisms as the sea urchin of figure 35, even when the individual is a single cell, its cytoplasmic body is composed of diverse parts; the three zones, with diverse functions, each producing a different part of the later body. What happens if one of these diverse parts is removed from the single cell? This has been done by cutting with a fine knife, or in other ways. When a certain part of the cytoplasm is thus removed, *the corresponding part is lacking from the body later produced.* Yet the cell from which this part was removed still contains the entire nucleus, with all the genes. It is clear that the individual is built up by the parts of its cytoplasm becoming diverse. A half of the cell that contains part of all the three cytoplasmic zones (in addition to the nucleus) produces an entire individual; while a half of the cell (with the nucleus) that lacks one of the cytoplasmic zones, produces a later individual that lacks the organs normally formed from that zone. In certain other animals (ctenophores), when any portion whatever of the cytoplasm of the egg is removed, a corresponding part is missing from the later body.

So it is clear that what a given cell shall later produce depends upon at least two diverse sets of conditions. We have just seen that it depends upon what cytoplasmic parts already produced are present in the cell. If all are present, the cell can produce an entire individual; if not all are present, the cell can produce only part of an individual. But, second, if all necessary cytoplasmic parts are present, what is produced by a given cell depends on its relation to other cells; that is, upon its environment. It will be useful to examine separately these two matters.

Dependence on Cytoplasmic Parts already Produced within the Cells

The sea urchin egg with its three zones divides successively into two, four, eight, sixteen cells (figure 35). In the two- and four-cell stages, each cell contains a part of all three zones; and each cell, if separated from the others, can produce an entire individual. But when the eight-cell stage is reached, the single cells no longer contain parts of all the three zones (figure 37, A), and they can no longer produce an entire individual. It is instructive to observe the effects of dividing the eight-cell stage in diverse ways. If it is divided into two halves, of four cells each, in such a way that each half contains all three zones (figure 37, B), each half will produce an entire individual. But if the upper four cells are separated from the lower four (figure 37, C, D), neither part produces an entire individual. The upper four cells yield an individual that lacks the skeletal structures and primitive alimentary canal which are derived from the missing lower two zones of the egg.

Such individuals do not develop far. The lower four cells yield an individual with skeletal structures and alimentary canal; but without the sense organ, mouth, and others parts that are produced from the missing upper zone of the egg. It is clear that what the cells produce depends upon what cytoplasmic parts they contain.

Similar results are observed when different parts of the ascidian egg are isolated; and the same is true for many other species. But in some species even if the right and left halves of the individual in the two- or four- or eight-cell stage are separated, each produces only a right or left half individual. The cytoplasm has become in some way set, so that even if the two halves are separated, they continue to develop as they would have done if they had remained together. Such is the case with the ctenophore (figure 38). It is a difference in cytoplasm of right and left sides that causes this result, not a difference in their nuclei. For if in the one-cell stage

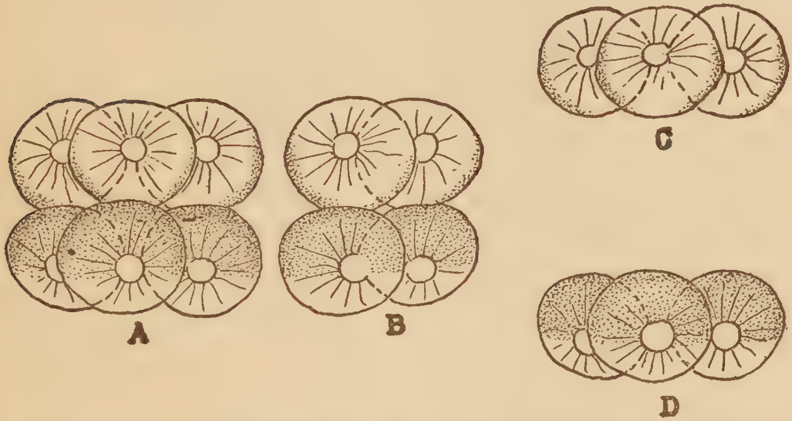


Figure 37—Diagrams to illustrate the effect of separating in different ways parts of the eight-cell stage in the sea urchin. A, eight-cell stage, showing the three zones (compare figure 35). B, Half of the eight-cell stage obtained by separating the right four cells from the left four. Such a half contains parts of all three zones, and produces a complete individual. C and D, the two halves obtained by separating the upper four cells (C) from the lower (D). Neither of these halves contain all the zones, and neither produces an entire individual.

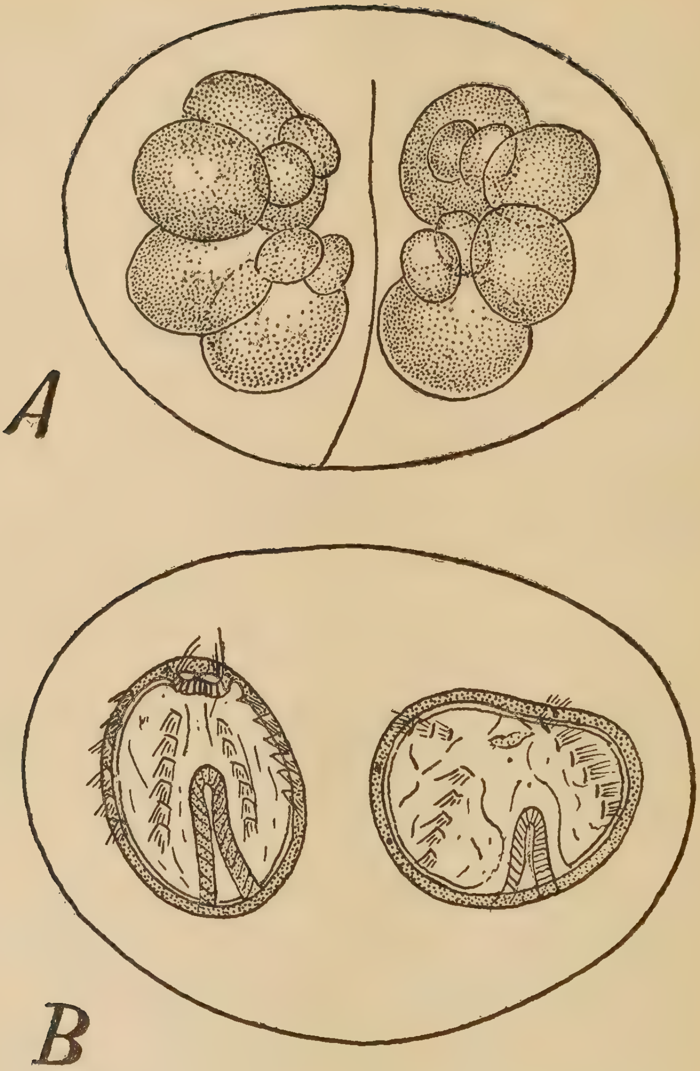


Figure 38—A, Cells of the right and left halves of a developing ctenophore egg, separated at an early stage. B, the two young half-animals derived from these half-eggs. The complete individual has eight rows of ciliary swimming plates; observe that each of the half animals has but four. After Fischel.

half the cytoplasm is removed (while the entire nucleus remains), only half a body is produced.

In many species of animals the different cytoplasmic parts do not become separated into clearly defined regions until much later in development, after many cell divisions have occurred. They long remain mixed together. If while in this condition a part of the cytoplasm is removed, the remaining part still produces an entire individual; for it still contains all the necessary cytoplasmic materials. In such organisms any part of the eight- or sixteen-cell stage can produce, if not too small, an entire individual.

Thus by isolating cells, entirely different results are produced in different cases—even from closely related species—depending on how fully and rapidly the different cytoplasmic materials become separated, and on how fully the cytoplasm is set. This caused great confusion in the early studies on the nature of development. The question was asked: If the first two cells produced are isolated, will each produce an entire individual, or a half individual? On the answer to this question appeared to depend the entire theory of development. If each isolated cell produces half a body, this would show, it was held, that development is a process of sorting out parts that correspond to the different later structures of the body. If each isolated cell produces an entire individual, some other theory of development is required; one in which adjustment to different conditions plays a great role; one according to which the organism uses whatever means may exist, to accomplish a certain end—the production of a unified individual.

When the matter was examined (the first successful work was by W. Roux and H. Driesch), some investigators found that one alternative was the correct one; others that the other was correct. Roux found that in the frog half an egg produces but half a body; Driesch that in the sea urchin half an egg produces an entire body. Other investigators differed in the same way; some found their experiments resulting as did those of Roux; others as did those of Driesch. There were long-continued controversies, till in time it became clear that the results are diverse for different species of animals; and that the differences depend on the rate and degree of separation of cytoplasmic parts, in the particular species studied. Development, it turned out, is not a process of sorting into diverse cells the different nuclear constituents, the different genes. On the other hand, it does involve a gradual sorting out of different kinds of cytoplasmic materials, which are produced under the action of the genes.

As development progresses further, the cytoplasm of the different parts of the organism becomes gradually more diverse, and more set, so that in time different tissues and different organs are produced. It appears beyond doubt that the increasing diversity of the cytoplasm is the result of continued interaction with the genes of the chromosomes. After each cell division the chromosomes absorb much cytoplasmic material, and become large vesicles forming together the nucleus(figure 34). They doubtless react with this absorbed material, changing it. Later, before the next cell division, this material is passed again into the cytoplasm, while the chromosomes reappear as minute structures. In this way the genes continually work over the cytoplasm, changing it, producing the bodily diversities.

Dependence on the Cellular Environment

But what happens in any cell, and what that cell produces, depends also on the environment of the cell: upon what other cells are in contact with it; and upon other surrounding conditions. This we have already seen for the early development of the starfish and sea urchin. It is remarkably shown in the development of frogs, salamanders, and other Amphibia. These animals produce eggs of a convenient size for study, varying from that of a small bird-shot up to that of a pea; and they readily develop while under observation in the laboratory. Parts of the egg can be removed, or parts of one egg can be transplanted to another, and the results observed. Methods have been found also for staining certain parts of the living egg, and by the color differences so induced it can be discovered what parts of the body are produced by particular parts of the egg.

Using such methods, it is found that in the Amphibia too, when the individual is still but a single cell, the cytoplasm is composed of different parts, with different functions in development. A certain part which in the eggs of some frogs is visible as a "gray crescent," initiates the developmental process, forming the beginning of what becomes the body. The remainder of the cytoplasm follows the lead of this, producing such parts of the later body as its relation to the gray crescent requires. The process of development is accompanied by division into many cells, each containing the nucleus with all the genes. At a certain time a hollow sphere composed of a great number of these small cells is produced, the *blastula* (figure 39 A). This transforms by a process of overgrowth of certain cells, into the spherical *gastrula* (figure 39, B). In these stages, experiments reveal most important facts as to the nature of development.

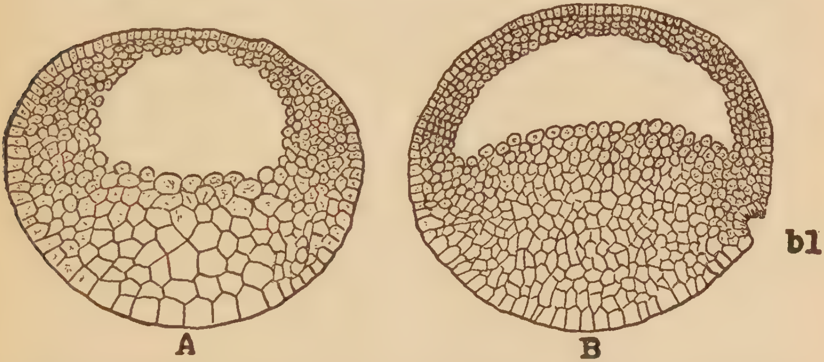


Figure 39—Early stages of development of the frog. A, Blastula; B, Gastrula, bl, blastopore, at the rear end. Just above the blastopore is the organization center, from which the developmental impulse passes upward and forward, organizing the different parts of the body. After Morgan, The Development of the Frog's Egg.

In the mass of small cells (figure 39), what part of the later individual will, in the usual course, be produced by each portion can be predicted with certainty. A certain set of cells can be pointed out as those that will produce the brain, certain others will produce eyes, others the spinal cord, the skin, the alimentary canal, and so on. It appears as if everything were fixed and determined; as if the fate of every cell were dependent merely on what genes or what kind of cytoplasm it contains.

But experimental study shows that this is not the case. If, in these early stages, from the region that is to produce the skin, a portion is removed and transplanted to the region that is to produce the brain, then the fate of the transplanted cells is changed. They alter their development, and become part of the brain instead of part of the skin. Or if the reverse transplantation is made, cells that would have formed a part of the brain alter their development and become part of the skin. What the cells become depends on their surroundings; on what the cells about them are becoming. Their development takes such a course as to fit into the general pattern; such a course that they produce structures which are fitted to the position in which they find themselves.

More precise study shows that what happens is essentially this: In the hollow spherical mass of small cells that constitute the gastrula (figure 39, B) there begins at a certain spot, just in front of the depression known as the *blastopore* (bl), some organizing or differentiating influence, of unknown nature, which passes from cell to cell, causing each cell to alter internally (through the interaction of its genes and cytoplasm, doubtless). Each cell alters in such a way as to fit it to the cells that have altered before it, so that all together they constitute the organized structural pattern of the embryo.

The region from which organizing influence passes is called the "organizer," or the "organization center." On tracing it back, it is found that this arises from the cytoplasmic region of the undivided egg that in the frog is called the gray crescent (mentioned in an earlier paragraph). From this organizing center of the gastrula the developmental impulse passes forward and outward in such a way as to cause each successive cell reached to transform into the next required portion of the pattern or structure. At a certain region the cells transform into the spinal cord; in front of these into the medulla, those next into the midbrain, then forebrain; at the sides into the eyes, farther forward into skin. But if before this has happened, this cap of cells that would thus transform is cut off and turned around, then replaced in any position in front of the organization center, the organizing and adjusting influence passes out from the organizing center in the same way and direction as before, without regard to the changed position of the cells. Now the cells that would have produced skin produce spinal cord; those that would have produced eyes now give rise to brain, and so of all the others. What each produces depends on its position with relation to the organizing center, and with relation to cells that have already become organized. It can be proved by such experiments, and by the transplantation of small areas, that any individual cell can take part in the production of any of the structures we have mentioned, or of many others.

By transplanting the organizing center itself, as has been done in many cases, by Spemann and his pupils, the embryo with its nervous system, eyes, etc., all in proper relations, may be produced in parts of the blastula or gastrula that would otherwise have produced none of these parts; or would have produced them in entirely different positions and relations. By transplanting a second organizing center to another region of an egg that already has one in the usual place, two embryos, each with eyes, brain, spinal cord, and the rest, are produced in the same egg.

Role of Adjustment to Conditions

Thus the evidence is complete that what a cell becomes, what line of development it follows, depends, not merely on what it has within it, but on its relation to the other cells; on its relation to the other parts of the embryo. The cells adapt themselves and their developmental processes to the conditions in the cells that constitute their immediate environment. Thus from the beginning development is adjustment to the environment; adjustment of the parts to each other. All the evidence indicates that each cell contains all the genes, all the possibilities that are given with the genes; but the genes alter their action on the cytoplasm, in dependence on the surroundings of the cell that contains them. The fate of the cells, in these early stages, is determined, not by different genes contained in different cells; not even, in the main, by the diverse cytoplasm contained in different cells, but by the conditions surrounding each cell. The same set of genes produces different things, follows a different course of action, under different surrounding conditions. This is the great and important fact which emerges from the study of early development.

Limitation of Power of Adjustment

But in time the genes interacting with the cytoplasm have produced definite cytoplasmic structures within the cells, as seen in the case of the egg of the sea urchin (figure 35). After this has happened, the cells so transformed can no longer produce any or all parts of the individual. Their fate has become fixed. Development is no longer adjustment to the conditions; or is less markedly such. Although the cells still contain all the genes, what these genes can do, what they can produce, is limited by the kind of cytoplasm that each cell contains. So in the frog and other Amphibia, after the differentiating influence from the organizing center has passed through the cells, the fate of the cells is fixed, or at least greatly limited. If now, at this later stage, parts are transplanted from one region of the embryo to another, the results are wholly different from those produced earlier. Cells that normally produce eyes will now still produce eyes, though transplanted to a region where eyes are wholly inappropriate. A set of cells whose prospect is to produce integument still produces integument, though transplanted to the region where a part of the brain is required. If a part of the embryo is now cut off, turned around, and replaced in position, it produces in the new position the same parts that it would have produced; though these are quite out of relation to the rest of the structures of the body. At a certain time, by the cytoplasmic transformations undergone, the cells have become limited as to what they can do. They can no longer be induced to change their course of development, so as to produce something else. At least this cannot be done readily, as it could when they were younger. Development has in the main ceased to be adjustment to the conditions surrounding the cells.

Detailed study shows that this process of fixing the fate of the different cells takes place in a series of steps or grades. At first in any cell the processes can be carried by the organizing influence in almost any direction; any cell may produce almost or quite any part of the later body. At a later stage the cell has become changed so that it can no longer transform into muscle or into part of the alimentary canal, though it may still produce any part of the nervous system or integument. Later yet the decision is made that it shall produce nervous system, but just which part of the nervous system is not yet determined. Later this is determined; the cell can now produce part of the eye, but not part of the spinal cord; and so on.

All these changes are seemingly matters of alterations in the cytoplasm, each cell still containing all the genes. There are indications that even after the cytoplasm has been partly transformed in a certain direction, for a certain period it has not become completely set, so that the change can be reversed, and the development of the cell carried in a new direction. But later, such reversal cannot be brought about, or certainly not readily.

Of course the possibility always remains that experimental methods may be found for reversing or transforming anew cytoplasm that has become fixed in a certain way; or that this may occur under some unknown conditions in nature. If by any means the cytoplasmic differentiations can be so reversed as to yield the condition present in the undivided egg, then, since all genes are present in each cell, presumably now the cell could produce any or every part of the individual. But so far as experiments have yet shown, at a certain period the fate of most of the cells has in the higher animals been fixed; what they shall produce has been determined.

Diverse Situations in Different Cells and in Different Organisms

Yet at the same period the different parts of the same developing individual differ in respect to this matter. In some parts at a given moment the fate of the cells has been fully determined. In others at the same time the fate has been determined only to the extent that they will form some portion of a particular organ system, such as the nervous system; though just which part of this will be formed is still alterable by changing the conditions. And other cells still retain almost or quite their early embryonic condition, so that they may transform into any one of many different things. In consequence, experiments in removing parts, or in transplanting them, give different results in the diverse parts of the same young individual. Some transplanted parts continue to develop just what they would have done if they had not been transplanted. Others change their method of action partly or wholly, and produce structures that fit the new surroundings. Many examples of these things could be given from the work of Spemann and others.

In different animals the rate and degree at which this permanent fixing of the fate of the cells takes place are very different. In some of the lower animals either the fate is never irrevocably fixed, or a large number of the cells remain in the original condition, scattered among those that have transformed into special tissues and organs. Then by removing parts of the individual, these cells whose fate has not been fixed ("embryonic cells") may be caused to begin development anew, producing once more the parts that were removed ("regeneration"). Even among many higher animals, such as the salamanders, this power of regenerating lost parts exists, even in adults, in a considerable degree. Either many cells have remained in the young, embryonic condition, or the cytoplasmic changes can be reversed in some of the cells, so that they may start anew on development.

Diverse Types of Developmental Processes in Certain Organisms

In most organisms that have been examined experimentally, development is of the type we have described. The genes interact with the cytoplasm and alter it, but do not themselves become changed; and each cell of the body contains all the genes. But relatively few organisms have been adequately studied as yet, and much remains to be learned of the nature of development. There are indications that in some organisms even the fundamental processes are of a different type from those above described; indications that the fundamental processes differ in different organisms. In certain worms, the Nematoda or thread worms, and in certain insects, appearances indicate that not all of the cells of the later body receive all the genes. The chromosomes of some of the cells in early stages of development are seen to break into pieces, and some of these pieces are absorbed and disappear. Other cells retain the entire chromosomes; these are the cells that later become the germ cells, which are to produce the individuals of the next generation. It seems probable that the cells which lose parts of their chromosomes no longer contain all the genes. But nothing is known experimentally as to the physiological effect of this loss. And the evidence is strong that in most organisms such loss of genes from particular cells does not occur; that on the contrary all the cells contain all the genes.

Summary on the Nature of Development

In sum, it appears that the fundamental process in developing the individual, producing its diverse parts and diverse functions, is the interaction of genes and cytoplasm. In this process the cytoplasm gradually becomes altered, until diverse tissue, diverse organs, have been formed. The cells of which these tissues and organs are composed all contain the same set of genes (at least this is the case in most organisms); but they differ among themselves in the constitution of their cytoplasm. The process of interaction is at first largely under the influence of the cellular environment, and other environment, so that development involves a continued adjustment to the conditions. Later, as the cytoplasmic constitution becomes set, the fate of the parts is fixed, so that the environment has little influence; adjustment to the conditions no longer occurs. In diverse organisms the details of these processes differ greatly; in some, even the fundamental processes appear diverse.

Additional features in the nature and processes of development are taken up in the next chapter.

NOTES AND REFERENCES ON CHAPTER III

1. Page 76. The account given in chapter III of the nature of the developmental processes is based mainly on the following papers and books:

A. Richards, *The History of the Chromosomal Vesicles in Fundulus and the Theory of Genetic Continuity of the Chromosomes.* Biological Bulletin, Vol. 32, 1917, pp. 249–291; J. Schaxel, *Versuch einer cytologischen Analysis der Entwicklungsvorgänge,* Dritter Teil, Zoologische Jahrbücher, Abt. f. Anatomie, Bd. 37, 1914, pp. 131–222; Th. Boveri, *Die Polarität von Ovocyte, Ei, und Larve des Strongylocentrotus lividus,* Zoologische Jahrbücher, Abt. f. Anatomie, Bd. 14, 1901, pp. 630–653; E. G. Conklin, *Karyokinesis and Cytokinesis in the Maturation, Fertilization and Cleavage of Crepidula and Other Gastropoda,* Journal of the Academy of Natural Sciences of Philadelphia, Vol. 12, 1902, pp. 1–121; and *Organization and Cell-lineage of the Ascidian Egg,* Journal of the Academy of Natural Sciences of Philadelphia, Vol. 13, 1905, pp. 1–119; S. Horstadius, *Über Determination des Keimes bei Echinodermen.* Acta Zoologica, Bd. 9, 1928, pp. 1–191; H. Spemann, *Ueber die Determinaton der ersten Organanlagen des Amphibien embryo,* Archiv für Entwicklungsmechanik, Bd. 43, 1918, pp. 448–555; and many other papers by Spemann and his associates in the same Journal.

An account of many of the researches on which chapter III is based will be found in: T. H. Morgan, *Experimental Embryology* (New York, 1927).

IV

THE NATURE OF DEVELOPMENT, CONTINUED

Different Development Due to Diverse Genes

THE preceding chapter dealt with the fundamental processes in the production of an individual; particularly the earlier processes. Further knowledge of the method of action of the genes in development is obtained by examining the differences produced by diverse sets of genes. Different fertilized eggs begin with different combinations of genes, and in consequence they produce individuals with diverse characteristics. How are these differences in characteristics brought about? Through what processes in development do diverse genes produce diverse characteristics?

Though knowledge on this matter is scanty, the results of breeding experiments throw some light on it. They yield the beginning of what will some time become a connected physiology of development in its dependence on the genes.

Diverse Periods at Which Genes Come into Action

Some genes are known to come into action at the very beginning of development, affecting the constitution of the egg that produces the new individual. In the silkworm, two races differ in the color of their eggs. One has eggs of a slate color, the other brown eggs. The difference in color is due to a differing gene pair in the two races. If the ova of the brown type are fertilized by sperm from the slate colored type, this makes no immediate difference to the color: the fertilized eggs remain brown. But when these (brown) eggs, containing a gene from the slate colored race, develop into females and these females produce eggs for the next generation, these eggs are all slate colored, like those of the slate race. And of the females derived from these slate colored eggs, three-fourths produce slate colored eggs, while one-fourth produce brown eggs, showing thus simple Mendelian inheritance, resulting from a single gene pair difference between the two races.

Another race of silkworms producing brown eggs differs from the race with slate colored eggs in another single gene. When the eggs of this "brown" race are fertilized from the "slate" race, they at once become slate colored and in later generations the two colors give simple Mendelian inheritance, the slate color being dominant. The color of the brown egg is quickly changed by the entrance of the gene from the slate race, showing that this gene comes into action at once.[1]

There are known other very early changes in development resulting from peculiarities of the genes, or chromosomes, that are brought into the ovum by the sperm. Many investigations have been made of the effects of fertilizing the ova of one species by the sperm from another species. Such experiments are readily performed with sea urchins. The earlier accounts set forth that in these animals all the earlier features of development were unaffected by the sperm; were thus determined by the mother alone. But more minute study, by Boveri, Fischel and Tennent, shows this to be a mistake. Various investigators have found that the type of sperm that enters the egg affects the rate of cell division, from the very start; affects the form of the cells in the blastula, the number of mesenchyme cells produced, the form of the gastrula, the color and form of the young larva, and the character of the skeletal structures that are early produced. Thus the nature of the sperm may affect the method of development from practically the very beginning. The same has been shown to be true for crosses between two species of fish, Fundulus, by H. H. Newman.[2] (In case the sperm belongs to some group of organisms not closely related to that from which comes the ovum, the sperm may not be able to act in the strange cytoplasm and so does not affect development at all. See Chapter XII, on the effects of crossing diverse organisms.)

Results of breeding experiments likewise show that certain particular genes come into action early in development. There occur in many organisms genes that are so defective as to lack some material that is necessary for development even to begin. The corresponding normal gene belonging to the same pair supplies this required material. Such deficient genes are called *lethals*. If we designate such a gene by the letter l, and the normal gene of the same pair by N, then if a fertilized egg has the pair NN, or Nl, it develops normally. But if it has both genes of this pair deficient, so that its constitution is ll, then it does not develop at all; the individuals that should occur are simply missing. Often there are such lethal genes in the X-chromosome. Since the male gets but a single X-chromosome, if this one has a lethal gene, the males die; while the females, having another X-chromosome that may bear the normal gene, live and develop. In the fruit-fly, a female often has thus a lethal gene in one of her X-chromosomes; not in the other. When such a female is mated to a normal male, her sons, as we know, all get their single X-chromosome from their mother. Half of them will get the X-chromosome bearing the lethal gene, and will therefore not develop. Thus the offspring show twice as many daughters as there are sons. Such results of breeding occur frequently in the fruit-fly. They show that the normal gene must come into operation at the beginning of development. When the necessary material it supplies is lacking, as it is in the lethal gene, development does not begin.

Other genes supply materials that come into activity at some time later in development. If such genes become altered so that they do not supply this material, development ceases at the point where this material is required, and the individual then dies. This is what occurs in the case of yellow mice. A gene present in normal individuals has become so altered that the mice produced are yellow in color. We may call this gene *Y*, while the corresponding normal gene may be called N. If the fertilized egg has for this pair of genes either NN or NY, the individual develops normally; though in the latter case its color is yellow. But if in the fertilized egg this pair is YY, so that the required normal gene N is lacking, then the individual develops only up to a stage when this normal gene must come into operation. It then dies; such dead "pure yellow" embryos are found within the body of the mother. There are indications that such imperfect genes are not uncommon, causing the death of embryos when a certain stage of development is reached; for dead young embryos are of frequent occurrence in some of the mammals.

A striking case of this kind is found in plants. Sometimes one of the genes that is required for the production of chlorophyll is deficient. It fails to supply some chemical that must enter into the chlorophyll, and the latter is not formed. The plants that have in this pair only genes of this deficient type do not turn green, but remain white. If we designate the normal gene, that supplies the required material, by the capital letter C, while the deficient gene is called c, then individuals having the constitution CC or Cc are normal, while those with the pair cc are white.

Chlorophyll is necessary for the elaboration of the nutrition of green plants, so that the individuals that have none cannot live beyond the stage in which their nutrition is supplied by materials stored up in the seed. Thus the individuals having the gene pair cc develop till they produce small white seedlings; these then die. They may however be kept alive by grafting them on green plants, which supply them with nutrition. Such grafted white plants may then produce pollen or ovules; and these when mated with ovules or pollen from green plants yield ordinary Mendelian inheritance, showing that the difference between green and white plants is due to a single pair of genes.

Certain genes come into operation only at a still later stage in development, when the groundwork for some particular organ is to be laid down. In the fruit-fly there is in the fourth chromosome a gene pair which may become so altered that the groundwork for the eye is not laid down. The flies having in this pair only the modified genes develop otherwise complete bodies, but are quite without eyes (figure 40, B). In those with the normal genes for this pair, on the other hand, the foundation for the eye is properly laid down; the individuals produced have complete eyes (figure 40, A).

Of some such nature are doubtless the changes that result in hereditary feeblemindedness in man. The brain is built up by the coöperative action of a great number of genes. When there is a defect in some gene pair that does a work essential for laying a proper foundation for the brain, the brain is left imperfect; it does not operate well, and feeblemindedness results. Such feeblemindedness is inherited according to the simple Mendelian rule.

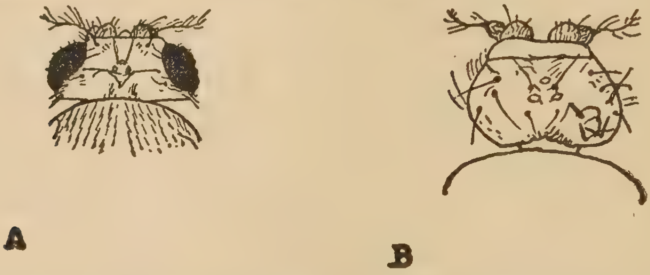


Figure 40—Head of normal (A) and eyeless (B) Drosophilas. The lack of eyes in B is due to a change in a single gene in the fourth chromosome. From the figures in Morgan, Bridges and Sturtevant, The Genetics of Drosophila.

Other genes are not required until a still later stage is reached. In the fruit-fly an eye may be laid down and partially developed; then if some gene is defective, development may take a wrong course. An irregular or deformed eye is produced. Many such cases are known in the fruit-fly. When a certain gene (situated near one end of the X-chromosome) is defective, no pigment is laid down in the eye, though it is otherwise well formed; what are called white eyes are produced. In other cases, defectiveness in a certain pair of genes does not prevent the laying down of pigment, but does alter the nature of this pigment. The pigment is then pink, or purple, or the like, instead of the usual red. A great number of such modifications of the eye color, resulting from changes in certain particular genes, are known in the fruit-fly. Each is inherited according to the simple Mendelian rule, showing that each is due to a change in a single gene pair.

The work of certain genes is essential for vigorous adult life. If such a gene pair is defective, the individual may develop to adult life, but it is weak, lacks resistance to bad conditions, and has a short life. Many such genes are known in the fruit-fly. Most of the genes that cause structural defects likewise make the individuals weak and short-lived, succumbing readily to unfavorable conditions. Raymond Pearl[3] has studied in elaborate detail the effect on length of life, rate of mortality and the like, of a number of such defective genes in Drosophila. In such cases long life and short life are inherited according to the typical Mendelian rule, or according to the rule for "sex-linked" inheritance. Long-lived individuals crossed with short-lived ones yield progeny that are long-lived. These bred among themselves yield progeny in which there are on the average three of the long-lived individuals to each short-lived one. The difference between long life with vigor, on the one hand, and short life with low vitality, on the other, is thus clearly due to a change in a single gene; one that supplies important constituents of the organism.

The instances above set forth illustrate the fact that the action of a particular gene is not limited to a particular part or constituent of the body. Many single genes produce far-reaching effects, influencing the entire constitution and functioning of the individual. They must act by producing certain substances which permeate the body, affecting all its parts. Others, so far as the evidence goes, are more limited in their action, producing substances that affect mainly certain definite parts of the body. Yet even these, it is found, usually exercise some general constitutional effect, so that Morgan has expressed the opinion that every gene affects the entire organism.

Through What Means Do Diverse Sets of Genes Produce Diverse Characteristics?

Light is thrown on the method by which such effects on diverse parts of the body, or on the entire constitution, are produced, by examining how different sets of genes produce some of the marked later diversities between individuals. The study of the production of difference of sex is particularly instructive; it brings to light a new class of processes in development. We may examine some features of the production of diverse sexes in mammals.

Production of Diverse Sexes

In mammals, as in many other organisms, individuals of the two sexes are diverse at the very beginning of development, when each is a single cell. They differ in their chromosomes. The female has an even number of chromosomes, a set of pairs. The male either has one less chromosome, so that the number is odd, or one of his chromosomes ("Y") is degenerate and nearly without function. That is, the male has an odd chromosome ("X") in place of the pair of X's that are present in the female (see Chapter II). All the chromosomes except the X's and the Y are, as we have seen, commonly called autosomes. Using this designation, we may say that the male has a double set of autosomes plus one X; the female a double set of autosomes plus two X's (figure 15).

A fertilized egg that contains the autosomes and the single X, since it produces a male, must of course develop very differently from an egg that has the autosomes and two X's, since the latter produces a female. How is this great difference in development brought about? How do the chromosomes operate in producing the difference of sex?

As the fertilized egg divides into 2, 4, 8, and finally into a great number of cells, we know that every cell of the male gets the autosomes plus one X, while every cell of the female gets the autosomes plus two X's. So every cell of the male differs throughout life from every cell of the female. We know that as development progresses, the chromosomes take in, modify, and give off again parts of the cytoplasm of the cells (see Chapter III). Since the result is different in the two sexes, the processes within the cells—the chemical changes—must be diverse, depending on whether one X is present or two.

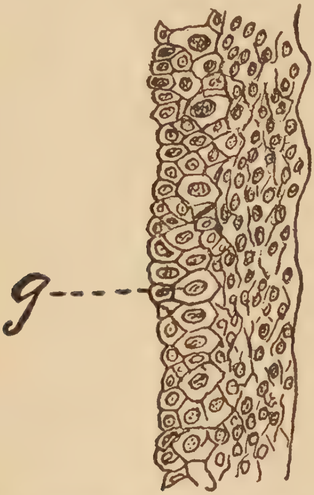


Figure 41—A portion of the germ gland at an early stage in the pig, showing the enlarged genital cells (g). Redrawn from part of a figure by Nagel, in Hertwig's Handbuch der Entwickelungslehre.

In mammals, at first the visible results of development are the same in the two sexes. For a considerable period the individuals of the two sexes cannot be distinguished. In the rat or rabbit, a young embryo is produced in which there is on the dorsal surface of the body cavity a strip or ridge composed of small cells (figure 41). These are later to produce the germ cells of the individual, the sperms or ova. This ridge is called the *germ gland.* Some of its cells enlarge; these are the ones from which the later germ cells will be produced; they are called *genital cells.* At first the germ gland is in its main features alike in the two sexes. But after a time appears the first difference that results from the presence of one X or two X's in the cells. The enlarged cells that contain but one X (in a male) divide and become small, forming the mother-cells for the later sperms. These are imbedded among the other cells of the gland, the so-called *interstitial cells.*

Meanwhile, at this same age, the germ glands of the individuals (females) that bear in their cells two X's have not changed. At this age, then, the male individuals are distinguishable by the groups of small cells; while the female individuals are like the very young males that have not changed.

Later, a change occurs in the females—the individuals that have the two X's. The large genital cells enlarge still farther, producing the mother-cells for the later ova; these are surrounded by a layer of small protective cells.

At this time, therefore, the individuals with but one X in their cells differ from those with two X's, in a way that can be detected by examining the germ glands. The two now continue to develop differently. The former produce the males, the latter the females. These of course differ tremendously in internal structure, in external features, in functions and behavior. The differences between males and females in such matters as colors, form of body, beard, horns, and the like, are familiar to everyone; they are known as the secondary sex characters.

Some of the means by which these later differences are brought about are revealed by certain experiments. If from a very young male the germ gland or testis is removed, the male secondary sex characters do not develop. The individual remains without beard, horns, or whatever may be the distinguishing characteristics of the adult male; it remains in the juvenile condition. And the same thing happens if the germ gland (ovary) is removed from a very young female; she remains juvenile in form and development.

This shows that the cells containing but one X produce the male secondary sex characteristics in some way through the mediation of the germ gland. For if the germ gland is removed, though all of the remaining cells still have the single

X, the characteristic male features are not produced. And the cells with two X's likewise produce the female secondary sex characters in some way by means of the germ gland or ovary.

How do the germ glands act in producing these results? Light is thrown on this by transplanting the germ gland of one sex to the body of the other, as has been done by Steinach, C. Moore, and others. From a very young female the ovary is removed and to its body a testis is transplanted. The testis continues to grow; and the female to which it was transplanted now gradually takes on the male secondary sex characters. In the same way, if from a young male the testis is removed and replaced by a young ovary, this male gradually takes on the female secondary sex characters.

It would appear therefore that the testis must secrete some substance that passes throughout the body, causing the latter to develop male characteristics. It has this effect normally on a body composed of cells bearing but a single X. But a similar effect is produced even when it acts on a body having two X-chromosomes in its cells—as occurs in the transplantation experiments. And parallel statements may be made for the ovary. The ovary must produce a secretion which, circulating through the body, causes it to develop female characteristics. And this result is produced not only in bodies having two X-chromosomes in their cells, but also in those having in their cells but one X. Such circulating secretions are known as *hormones*.

It would be of great interest therefore to cause the blood from a male to circulate in the body of a young female; this should cause the young female to develop male characteristics. This experiment has been performed in nature, in what are known as free martins, in cattle. The matter has been fully studied by F. R. Lillie.[4] Cattle at times produce a pair of twins, one of which is a male, while the other shows a mixture of the characteristics of the two sexes. The latter is known as a free martin. Lillie found that in all such cases the blood systems of the two developing individuals are in communication. As set forth in a previous paragraph, in the mammals the male develops its peculiarities earlier than the female. So at a certain time blood from a partially developed male flows through the body of an undeveloped female. This blood, bearing the secretion from the testis of the male, causes the body of the female to develop many of the male characteristics. The result is to produce from the original female a "free martin," having a mixture of male and female characteristics. The transformation is never quite complete, and the same is true of the results in transplanting testes and ova, described in earlier paragraphs. The originally female body, having two X-chromosomes in each of its cells, always develops some of the female characteristics, some of the female structures, along with the male ones. Apparently the cells with two X-chromosomes react to the male hormone in a way somewhat different from the reaction of the cells with but one X-chromosome. Thus the sex characters depend mainly on which hormone is present; but partly also on the number of X-chromosomes present in the cells on which the hormone acts.

Hormones in Development

It appears then that the original chromosome difference between male and female eggs produces many of its effects through the agency of diverse secretions in the two cases. Such secretions, produced by one part of the body, circulating to other parts, and there producing an effect, are known as inner secretions, endocrine secretions, or hormones. The germ gland in which the cells have but a single X-chromosome produces one type of hormone, inducing the development of male characteristics. The germ gland whose cells bear two X's produces another type of hormone, inducing the development of female characteristics. Male and female characteristics depend ultimately on the difference in chromosomes between the fertilized eggs from which they came. But this dependence is mediated through the different hormones produced by the different chromosome combinations.

The conditions described above are those found in mammals. In birds the situation as to the production of sex characteristics differs greatly from that found in mammals. Hormones play a part, but their role differs from that which they play in mammals. In insects sex differences seem not dependent on hormones, but to result in some more direct way from the original diversity of chromosomes between the two sexes. The physiology of different groups of organisms may differ as much as does their structure. Details for the birds and insects will not be entered upon here, since our purpose is only to illustrate the various means by which the chromosomes operate in development; of these, hormones form an important class.

Besides the germ glands, other parts of the developing body produce hormones that circulate through the entire body and affect the development or the physiology of other parts. The study of these hormones is one of the modern branches of biology, which has aroused very great interest. To their action enormous importance has been attributed, particularly in determining the temperaments and mental characteristics of human beings. Some of the chief organs of inner secretion are, besides the germ glands, the thyroid gland, the parathyroids, the suprarenal bodies, the pituitary body or hypophysis. The nature of the action of inner secretions in development, their importance and their limitations, will best be appreciated by examining the action of the hormone from the thyroid in the development of the Amphibia; for here such action has been studied much more completely than anywhere else.

Hormones in Amphibian Development

In all classes of Amphibia (with rare exceptions in certain species), there develops from the egg a tailed swimming creature, with gills, and at first without limbs: the tadpole. In that group of the Amphibia which includes the toads and frogs, at a certain period the tail and gills are lost, legs develop, there is an internal and external transformation, and the tadpole metamorphoses into the four-legged frog or toad. What brings about this metamorphosis? J. F. Gudernatsch[5] found that if very young tadpoles are fed pieces of the thyroid gland, they quickly metamorphose into frogs, even though as yet extremely small. In this way frogs as small as flies were produced. Tadpoles of the bull-frog, that usually do not metamorphose till two or three years old, were thus caused to metamorphose during the first season of their existence, and within two weeks of the time that the feeding of the thyroid was begun.

On the other hand, it was found that if the thyroid gland was removed by an operation, the tadpoles do not metamorphose; they remain in the form of tadpoles, although they grow large, and may become sexually mature.

The study of this matter was taken up by many other investigators, and much has been learned as to the effect of the thyroid on development in Amphibia. W. W. Swingle [6] found that the effect of the thyroid is largely due to the iodine that it contains. Iodine fed to tadpoles with the food caused metamorphosis, as did the feeding of thyroid.

The thyroid gland produces an inner secretion or hormone, that contains iodine, and that passes into the blood and so circulates through the body. The iodine that it contains is united with certain organic compounds, and some of the effects of its secretions are not producible by iodine alone; this is particularly true of its effects in higher animals.

The thyroid, like other parts of the body, develops gradually, and in the early stages of its development it does not produce its secretion. It remains thus inactive even past the time when the remainder of the body has become capable of reacting to its secretion. But at a certain period it begins to produce its characteristic secretion, and to pour it into the blood. And as a result the tadpole transforms into the frog or toad.

Diverse Parts React Differently to the Same Hormone

When we examine how this transformation occurs, we discover certain things about the action of the thyroid hormone that are of great interest for the understanding of development. We find that different parts of the body are affected in very different ways by the same hormone; that under its action each part of the body has its characteristic way of reacting. And we find that different races or species are affected very diversely by the same hormone. The effects of the hormone are therefore by no means due alone to its own peculiarities; equally important is the constitution of the part on which it acts; of the race on which it acts. These important relations are remarkably illustrated in the different Amphibia.

The most general effect of the pouring of the thyroid hormone into the blood is to accelerate greatly the metabolism of the young tadpole—the chemical processes occurring in the body. When the tadpole is fed an excessive amount of thyroid, it loses weight rapidly. The bodily tissues tend to be destroyed and absorbed and the process may go so far as to produce death, with symptoms similar to those resulting from starvation. In the natural transformation of the tadpole into the frog the thyroid hormone acts in this same way on the gills, on the tail, and on parts of the intestine. The gills and tail break down and are absorbed, quite disappearing. Much of the long coiled intestine disappears in a similar manner, leaving only the short intestine found in the frog.

But on other parts of the body no such effect is produced. The limbs, under the action of the thyroid hormone, not only do not fade away, but on the contrary grow rapidly, soon becoming large. Not only do they grow, but they develop different parts, toes, joints, and the like; and proceed to function actively. Also, lungs are now produced. Development of the body takes a different course from that before followed, so that the entire form is changed. The sex glands, the testis and ovary, are neither destroyed, like the gills and tail, nor hastened in development, like the limbs; they continue to develop much as they were doing before the thyroid hormone came into action.

Why do different parts of the body, different cells, thus react differently to the same hormone? We know that all the cells contain the same set of genes, so that the different behavior is not due to diversity of genes in the cells. But we know also that the cytoplasm has become diverse in the different cells, through its interaction with the genes, under the particular organic environment of each cell. It appears probable, perhaps certain, therefore, that the diverse reactions of different parts to the same hormone are due primarily to the diverse cytoplasm in the cells of these parts. This is a relation which, if valid, is of great significance for many phases of development.

Thus each part or tissue has its own way of reacting to the thyroid hormone, so that different results are produced in different parts of the body. Some parts are reduced and destroyed, others transformed, others caused to grow and differentiate; others are unaffected. No single definite action on development can be attributed to the hormone; the effects produced depend as much on the constitution of the parts acted upon as on the nature of the hormone. The diverse parts so react as to yield complex specialized results playing an important role in the life of the animal. The tadpole, fitted for life in the water and for feeding on vegetable food, is transformed into a creature adapted to a land life, and to feeding on animal food.

Diverse Species React Differently to the Same Hormone

Not only do different parts of the same body behave differently under the action of the same thyroid hormone, but it is also true that different species of amphibians respond diversely to it. Besides the frogs and toads, which lose their gills and tails and come out on land, there are salamanders and newts whose life takes a very different course. Such salamanders as Amblystoma (figure 42, B) have a tadpole stage much resembling that of the frog. When such tadpoles are subjected to the thyroid hormone, they transform, losing their gills, but not their tails. Their limbs are not caused to develop faster than before (as they are in the frogs and toads). The salamander retains its elongated form, but acquires lungs and may creep out on the land. In another group of the Amphibia, exemplified by the "mud puppy," Necturus, there is no transformation; the gills are never lost; so that the creatures remain throughout life in a condition corresponding to the tadpole stage, though they grow large. It might be supposed that the failure to transform is due to the lack of a thyroid hormone. But this is not the case. If they are fed thyroid or otherwise subjected to it, in ways that cause the transformation of frog tadpoles, they do not transform, but retain gills and legs as before.

The axolotl (figure 42, A) is a salamander that is in some degree intermediate between the Amphibia that transform and those that do not. Usually it retains its gills throughout life, living in the water, where it lays eggs and produces young. But if the axolotl is fed on thyroid, it metamorphoses, losing its gills, changing the form of the body, and becoming an Amblystoma (figure 42, B). Yet its usual failure to transform is not due to the lack of a thyroid. Examination shows that the axolotl has an active thyroid, which causes transformation when it is transplanted to a frog tadpole. Why then does the axolotl usually not transform? This question has not been answered with certainty. Probably there is some mechanism that prevents the secretion of its own thyroid from getting into its blood. The case of the axolotl illustrates the fact that the effect of the thyroid hormone depends upon other peculiarities of the animal, aside from the mere possession of the thyroid and its hormone.

The effect of the thyroid hormone thus differs greatly in different animals. The cells in different species have different constitutions, diverse genes; and they react diversely to the same hormone; just as diverse parts of the same individual react diversely to the same hormone. The effect produced depends as much on the constitution of the cells acted on as it does on the nature of the hormone.

In man the thyroid hormone has a very great effect on development, though of course one that differs much from its effect in Amphibia. Some human individuals have the thyroid little developed, so that the hormone is nearly lacking. Such individuals do not develop normally. They remain small; and the body form is abnormal, some parts being more prominent than usual, others less. The brain does not develop properly, so that an idiotic dwarf, known as a cretin, is the result. When this repulsive creature is fed thyroid for a long time, gradually the abnormal features disappear; growth proceeds in the usual way, the brain develops properly, and the helpless idiot becomes a normal child, with the normal intelligence. When the thyroid is removed from a young mammal, such as the sheep, the latter develops many of the peculiarities of the human cretin.

If in place of being inactive or lacking, the thyroid is overactive, the individual is slender, underweight, energetic, active and nervous. There is a high rate of heart beat, high blood pressure, and excessive production of heat. The peculiarities appear to result from the high rate of metabolism produced by the thyroid hormone.

Different individuals vary greatly in the activity of the thyroid, and to this doubtless many of the differences in temperament are due. The differences in the thyroid function are due in some cases to diverse environmental conditions. Lack of iodine in the food or drinking water may result in imperfect thyroid hormones, with the consequent abnormal development. In many cases the diversities in the thyroid function are doubtless due to original differences in the genetic system with which the individuals begin life. The genes bring about many of their effects through the thyroid hormone which they produce; as they do others through the sex hormones. Diverse sets of genes produce thyroid hormones differing in quality or quantity, thus causing differences in the characteristics of the individuals.

Other hormones play important roles in development, though the effects of others have been less studied than those from the sex glands and from the thyroid. The parathyroids, small glands imbedded in the surface of the thyroid, are necessary for normal development, through their control of the amount of calcium in the blood. The suprarenals influence greatly the development of the secondary sex characteristics; and their secretion has an important role in the functioning of the body. The pituitary gland, lying at the base of the brain, produces two hormones, both having important effects in development. The hormone from the anterior lobe of the gland promotes growth; if its action is excessive, growth goes beyond the usual state, and giants are produced. If on the other hand this hormone is inactive, the individual remains small and undeveloped. Excessive action of this pituitary hormone has been found also to cause rapid and excessive development of the ovary, while if the hormone is lacking the ovary degenerates. The hormone of the posterior lobe of the pituitary has an effect on nutrition; it promotes the production of fat.

It has been suggested that differences between the races of men may be due mainly or entirely to differences between particular hormones; and the same suggestion is made for the greatly differing races of dogs. Some have the characteristics to be expected if the thyroid secretion is scanty and inactive; others, those that go with an active thyroid; and similarly of other hormones. One must not, however, in the absence of experimental tests, be too confident of the correctness of such suggestions. The differences between the salamanders that keep their gills throughout life, and those that do not, are of just the sort that might be expected from differences in their thyroid secretion, yet experiments show that they are not due to this cause. Cells with different kinds of cytoplasm (produced in development), and cells with different original constitutions, different genes, respond very differently to the same thyroid hormone, as the experiments with Amphibia clearly show. This is one of the capital facts of development; it must never be left out of consideration. Diverse races of men, and of dogs, certainly begin life with different sets of genes. Many of their diverse characteristics are due to this fact, whatever the nature of the thyroid or other hormones present. The diversity of hormones, if it exists, is due to diversity of genes; and with genes diverse the same hormones produce different effects. Different hormones acting on a given set of genes yield diverse characteristics; the same hormones acting on different sets of genes also yield diverse characteristics. Such situations recur everywhere as we study the effect of different factors on characteristics and development.

Hormones as Intermediate Steps Between Genes and Developed Characteristics

In sum, it is clear that many of the effects of the genes in development are produced through the action of the hormones that they manufacture. Particularly in later development the hormones play a very great role. Diverse sets of genes produce hormones differing quantitatively or qualitatively, and to these differences many of the inherited peculiarities of individuals are directly due. The diverse characteristics are due originally to diversity of genes, mediately to diversity of the hormones produced by the different sets of genes.

Hormonic and Environmental Action

The action of hormones reveals again that what a given set of genes produces depends not on its own constitution alone, but on the conditions surrounding it. Such a relation was revealed also in the earlier stages of development: what a given cell produced depended on the cells that surrounded it. If a hormone of a certain quality or intensity of action is present, the cells produce a certain set of structures; if the hormone is of another quality or intensity, the same cells produce other structures. The same set of genes yields the male or the female characteristics, depending on what hormone is present. The same set of genes produces a giant or a dwarf, depending on the hormone present. The same set of genes yields a lethargic or an active individual, an imbecile or an intelligent person, depending on the hormone that is present. What hormone *is* present depends again, under the usual conditions, on what set of genes was present at the beginning; but by operations, or in other ways, another hormone may be substituted for the one normally present, changing development. Through the hormones they produce, the diverse parts of the body affect each other's environments, altering development, causing each part to develop in relation to others. The course of development of any part is largely a reaction to the environment of that part.

But what is the effect of the outer environment of the individual on all this? The environment thus far dealt with has been that of the cells within the body; the internal environment, as it is sometimes called. This determines in large measure what set of characteristics, out of several possible sets, shall be produced by any particular set of cells. Is there any similar action of the external conditions met by the individual? To what extent do characteristics and development depend on external conditions? This is the question dealt with in the next chapter.

NOTES AND REFERENCES ON CHAPTER IV

1. Page 103. The facts as to the dependence of the color of the eggs of the silkworm on genes are taken from the paper of Y. Tanaka, *Maternal Inheritance in Bombyx mori,* Genetics, Vol. 9, 1924, pp. 479–492.

2. Page 103. See H. H. Newman, *Further Studies on the Process of Heredity in Fundulus Hybrids.* Journal of Experimental Zoology, Vol. 8, 1910, pp. 143–161.

3. Page 107. See R. Pearl, *The Biology of Death,* 275 pp. (Philadelphia, 1922).

4. Page 111. See F. R. Lillie, *The Free Martin; a Study of the Action of Sex Hormones in the Foetal Life of Cattle.* Journal of Experimental Zoology, Vol. 23, 1917, pp. 371–452.

5. Page 113. See J. F. Gudernatsch, *Feeding Experiments on Tadpoles.* Archiv für Entwicklungsmechanik, Bd. 35, 1912, pp. 457–483.

6. Page 114. See W. W. Swingle, *Studies on the Relation of Iodine to the Thyroid.* Journal of Experimental Zoology, Vol. 27, 1919, pp. 397–425; and many other papers in the same journal by this author. These will give references to other investigations in this field.

V

ROLE OF ENVIRONMENT IN DETERMINING THE CHARACTERISTICS OF INDIVIDUALS

What the Genes of a Cell Produce is Determined by the Internal Environment

WHAT part in producing the characteristics of individuals is played by the experiences that they meet in life; by the outer conditions that act on them as they develop? In preceding chapters it has been shown that the characteristics produced depend on the genes with which the individual starts, in the sense that different sets of genes give rise to very diverse individuals. It has also been shown that what any particular cell of the individual produces is largely determined by the surroundings of that cell—by the cells in contact with it, and by the hormones that bathe it; in short by the "internal environment"—so that the same set of genes produces different results in different cases. May this be true of the individual as a whole? May the same sets of genes produce different types of individuals, depending on the conditions that they meet?

Application to Individuals as Wholes

It has already been seen that this question must be answered in the affirmative in so far as the hormones affecting the individual are changed. An individual that would normally become a female is largely transformed into a male, if the male hormone is caused to circulate in its body, or if its ovary is removed and a testis transplanted to it. An individual that would otherwise become an imbecile, a cretin, is caused to become a normal intelligent person if fed upon thyroid. In such cases, products of the genes are transferred from one individual to another, and in the latter the same effect is produced as would result if the hormone came from the individual's own genes.

Hormones Producible Outside the Body

But can these substances affecting development be produced in any other way than by the genes within the cells? Again the answer is Yes. The active principle of the thyroid has been synthesized; the substance so produced may be used in place of that produced by the genes, with the same effect on development and characteristics. Similarly, one of the hormones from the suprarenal capsules has been produced artificially; and long steps have been taken toward synthesizing insulin, the hormone produced by the pancreas. A vast amount of work is in progress in this direction.

Man is just at the beginning of his knowledge and power in this field of work. The advances just mentioned in the laboratory preparation of products of the genes have all come in the last twenty years; most of them in the last five years. How far will men have advanced in this direction in the next one hundred years? In the next one thousand years? The door for advance in the control of development from outside is wide open; what is not possible now may soon become possible.

These things make it clear that the processes of development, which determine what characteristics shall result, are not closed off from outside control.

Does the External Environment Affect What the Genes Produce?

But does anything of this sort occur under natural conditions? Is the development of an individual influenced by the outside conditions that it meets, so that under different conditions different characteristics result? Obviously there would be in this nothing opposed to the rest of our knowledge of biology; on the contrary it is what should be expected. Many characteristics depend upon the hormones produced by the genes. The production of hormones might be under the influence of the nervous system, and through that means under the influence of outer conditions; or, outer conditions might affect hormone production in some still more direct way. In either case the characteristics determined by the hormones would be under the influence of the outer conditions.

It is known that the production of some of the hormones is indeed under the influence of the nervous system, and through it is profoundly affected by outer conditions. This is notably the case with one of the hormones produced by the suprarenal capsules. This hormone profoundly affects the behavior of the individual. Little is known in detail of such action of the nervous system on the hormones that affect development. Yet in one of the Amphibia a very great and striking effect on development and on the adult characteristics is produced at times through the action of external conditions, almost certainly through their action on the thyroid. The axolotl, mentioned in the preceding chapter, is a large salamander that has prominent red external gills, a tail adapted for swimming, and other bodily features that fit it for living in the water (figure 42, A). In the water it may thus live all its life, becoming mature, producing eggs and offspring, and finally aging and dying as an aquatic animal.

But, as we saw, if the young axolotl is fed on thyroid, it undergoes a tremendous transformation, comparable to that which changes a tadpole into a frog. It loses its gills; its body form alters in every detail, so that it is no longer adapted for swimming. It crawls out on the land and becomes the land salamander known as Amblystoma (figure 42, B). Its characteristics have become completely changed. On land it lives for the rest of its life, going to the water only to lay its eggs.

It is found that external conditions may induce this same transformation. If the axolotl is gradually forced to leave the water and to exist on land, under certain conditions of temperature and the like, it transforms into an Amblystoma, as it does when fed on thyroid. There is little doubt that what this

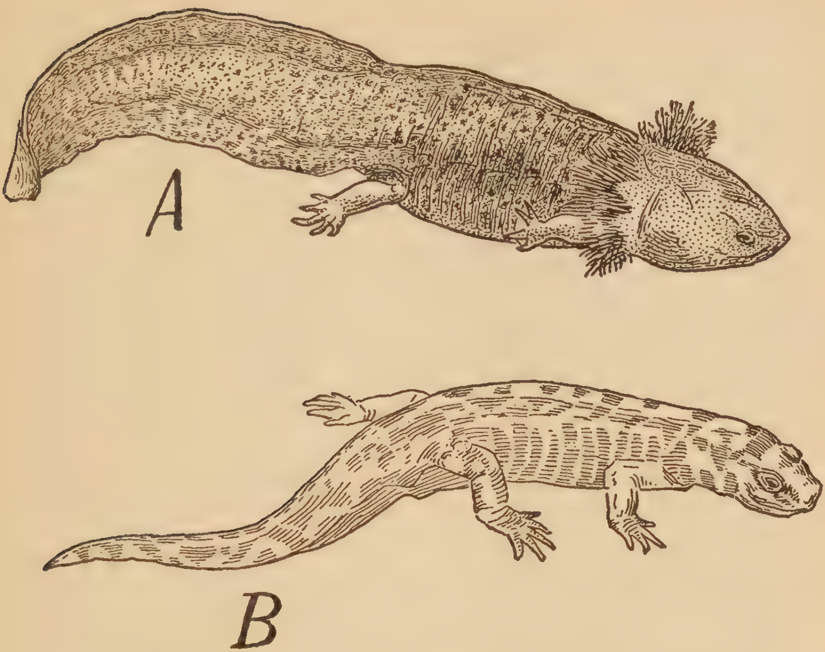


Figure 42—Axolotl (A) and Amblystoma (B), to show the differences in form and structure. Figures modified from those in Brehm's Thierleben (1912).

change of conditions does is to cause the animal's own thyroid to throw its secretion into the blood, and that this then induces the transformation into Amblystoma. This however has not been experimentally proved.

Clearly, this animal may have either one of two extremely diverse sets of characteristics, depending on the conditions that it meets. The difference is as great as that between an uncultured human being and a cultured one. It is not improbable that many effects of environmental conditions on the characteristics of organisms are due to the immediate effects of the surrounding conditions on the production of hormones.

If chemicals produced by the organism's own genes have so great an effect on its characteristics, may there not be other chemicals, otherwise produced, that have such effects? That there are such other chemicals, greatly altering the characteristics of individuals, is shown by modern work on nutrition. This has discovered that there are, in various foods, substances known as vitamins, that have effects comparable to those of hormones. The developing organism must take these vitamins with its food; otherwise it ceases to develop; or development takes an abnormal course, and highly defective individuals are produced. Butter, various animal fats, and the yolk of egg contain a substance known as Vitamin D, which is needed for the proper development of the bones, particularly if the individual is not exposed to sunlight. If the food does not contain Vitamin D, calcium is not properly deposited in the bones. These therefore remain cartilage; they bend under weight, and in time become fixed in their distorted condition, so that the individuals have crooked limbs, bow-legs, or various bodily malformations. The disorder which results in such effects is known as rickets. If food containing Vitamin D is supplied, rickets disappears, development takes its normal course, and if the injuries already produced have not gone too far, they may be cured. Of extreme interest is the fact that an outer condition, sunlight, has the same effect as does Vitamin D. If the developing individual is exposed to sunlight, the bones develop normally, and rickets may be cured, even if Vitamin D is present in so small a quantity as to be ineffective without the sunlight. Children receiving little sunlight must have more Vitamin D; children receiving little vitamin D must have more sunlight.

Oranges, tomatoes, and various other fruits contain another substance, Vitamin C, which is required for normal development. Infants whose diet does not contain it fail to gain in weight, their nutrition becomes disordered, other troublesome symptoms appear, and there is a high susceptibility to infections. All these troubles quickly disappear on the administering of orange juice or other food containing Vitamin C in proper amounts. In adults the lack of Vitamin C produces scurvy; it is prevented or cured by the use of fruit juices.

Another substance, Vitamin E, present in various leafy vegetables and certain cereals, is necessary for the development of young rats beyond an early stage. If the diet of the mother does not contain this substance, the young die within the mother's body, between the twelfth and twentieth days of development. This same vitamin is required at a later stage of development for the production of germ cells by males. If their diet contains none of this vitamin, the males grow to maturity and appear normal, but are completely sterile, their germ cells degenerating.

Other vitamins are known to be required for normal development and functioning. Knowledge along these lines is increasing rapidly.[1]

The facts as to the vitamins and their effect on development show that not all the substances required for normal development are elaborated through the action of the individual's own genes. Besides the hormones, produced within, the vitamins, coming from outside, profoundly affect the nature of development, and the characteristics of the individuals produced.

Natural Conditions Affect What the Genes Produce

In organisms as we find them in nature, are the characteristics of the individuals altered by the external conditions under which they live, the physical and the social conditions that affect them? May diverse characteristics result from diverse outer conditions? In other words, are the products of the interaction of the genes and cytoplasm different under different external conditions?

This question too requires an affirmative answer. Innumerable examples can be given of the alteration, by environmental conditions, of the characteristics produced by genes; characteristics that are inherited in the typical Mendelian or sex-linked ways; the so-called hereditary characteristics. The role of environment differs greatly with respect to different characteristics. Some as we find them are little altered by the diverse environments to which they are commonly subjected, while others are greatly altered (a matter to be dealt with later). But in principle there is no opposition between influence of genes and influence of environment, on the same characteristics. This may be illustrated by a number of typical cases:

Examples of Environmental Action on Gene Products

R. A. Emerson [2] found that different colors in maize plants are typically hereditary. When the plants are cultivated in fields under the usual sunlight conditions, some of them are reddish (in flowers, leaves and other parts) ; others are green, without tinge of red. Cultivated separately, each type perpetuates itself. The red plants produce red offspring, the green plants green offspring. If green and red plants are crossed, the two colors are inherited in the typical Mendelian manner, showing that the difference in color depends upon a difference in genes.

But the color depends also on the environment. The genes that produce red do so only in the sunlight. Thus plants having such genes are red only if grown in the sunlight; parts grown in the shade are green. So, of two plants with the same genes, one may be red, the other green, and the difference is environmental; it is due to the different conditions under which they have lived. Of two other plants that have lived under the same sunny environment, one will be red, the other green; and in this case the difference is due to their diverse genes. The same difference that in one case is produced by diversity of genes is in the other case produced by diversity of environment.

Again, two plants of the red variety differ in color if one is grown in the sun, the other in the shade. But two plants of the green variety, grown one in the sun, the other in the shade, do not differ in color. Thus whether the environment shall produce a certain effect depends on what genes are present. Conversely, whether a difference in genes shall produce an effect may depend on the environment. Two plants, one of the red variety, the other of the green variety, differ in color if grown in the sun, but not if grown in the shade.

Emerson found many other color variations in corn that are due to diversity of genes. There are purple varieties, brown varieties, several types of green varieties, several types of reddish varieties. These different color varieties react very differently to sunlight and shade; some are altered, some are not. There are also other environmental conditions that affect the color. Growth on poor soil tends to produce the red color in some varieties, not in others. Storage of carbohydrates in the tissues produces red color in plants with certain types of genes, not in those with other types. The situation in maize illustrates in a most instructive way the varied interactions of genes and environment, and the great diversities in these interactions among different races of the same species. Whether the environment shall produce a given effect depends on the genes that are present at the beginning. Whether the presence of certain genes shall produce an effect depends on the environment in which the plant lives.

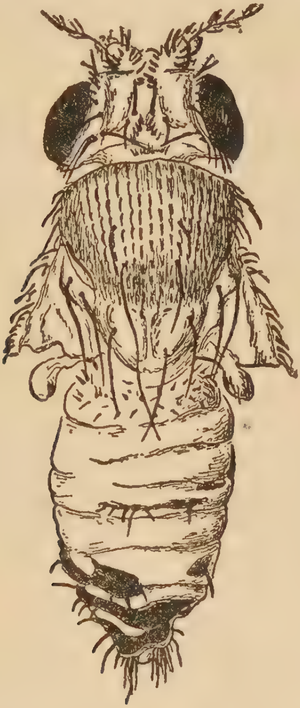


Figure 43—Abnormal abdomen in Drosophila; a characteristic resulting from a defective gene in the X-chromosome, but manifested only when the organisms are grown in a moist atmosphere. (The wings have been removed, to show the irregularity of the abdominal segments). After Morgan and Bridges, 1916.

Certain characteristics in the fruit-fly illustrate similar relations between the effects of genes and the effects of environment. Drosophila is commonly grown for experimental purposes in bottles containing decaying banana, the atmosphere within the bottles being moist. When so grown, certain individuals are defective in that the abdomen is ill-formed; the segments are not regularly and sharply marked off (figure 43). This abnormality is found to be due to a defect in a gene of the X-chromosome, so that it shows sex-linked inheritance, the abnormality being dominant. For example, when normal females are crossed with abnormal males, all the daughters produced have the abnormality, while all the sons are free from it.

But the abnormality depends also on the environment. It appears, in the individuals having the defective gene, only if they are grown in a moist atmosphere. If grown in a dry atmosphere, the individuals are normal, even though they contain the defective gene. The production of the abnormal abdomen thus requires both a certain type of gene and a certain type of environment. When grown in a moist environment, the difference between normal and abnormal individuals is due to a gene difference, or as it is usually put, to heredity. If the defective gene is present in all the individuals compared, the difference between normal and abnormal individuals is due to an environmental diversity; to moisture or dryness.[3]

Another defective gene in Drosophila causes the animals to produce "reduplicated legs" (figure 44). Certain joints of the legs, or certain entire legs, are doubled. This again is due to a gene in the X-chromosome, so that the abnormality shows sex-linked inheritance. But even when the defective gene is present, the abnormality does not appear if the animals are cultivated in an adequate degree of warmth. In the cold, individuals with the defective gene have reduplicated legs, individuals with normal genes do not. Among individuals with the defective genes, those kept in the cold have the reduplicated legs, those kept warm do not. Like abnormal abdomen, this peculiarity requires for its production both a certain type of gene and a certain type of environment. The same difference that is produced in some cases by diversity of genes is produced in others by alteration of the environment.[4]

These cases illustrate the fact that an inherited defect need not be one that is inevitable, inescapable, as is sometimes imagined. The mere fact that a defect is hereditary does not mean that it must occur. What is inherited is a constitution, a set of genes, that under certain conditions will produce a certain defect; under other conditions it may not.

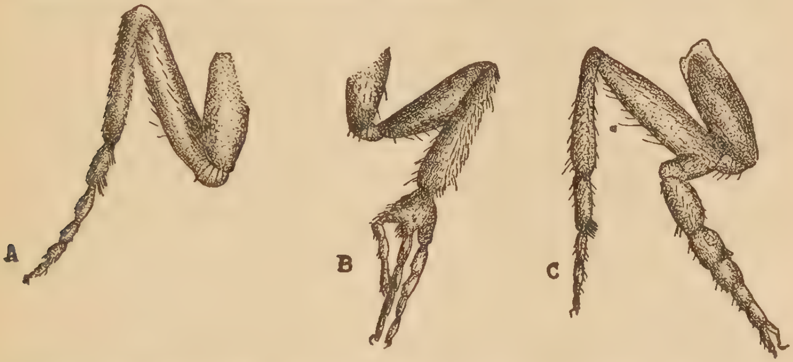


Figure 44—Reduplicated legs in Drosophila, a characteristic resulting from a defective gene in the X-chromosome, taken in connection with development at a low temperature. A, normal first leg; B and C, legs showing different types of reduplication. After Hoge (1915).

In the fruit-fly, as in other insects, the eye is of the compound type, containing normally about 800 separate elements. Each element shows on the surface of the eye a small elevated facet, so that there are about 800 facets. But in some cases some of the elements of the eye are imperfect, so that there are less than the usual 800 normal facets. The number of normal elements or facets present depends both on peculiarities of the genes, and on the environmental conditions. The situation is somewhat complex, but illustrates most instructively the relations of genes and environmental conditions to characteristics.

Some individuals have at the point 57 in the X-chromosome an abnormal gene, commonly known as the "Bar" gene (previously mentioned in another connection). This reduces the number of perfect facets in the eye, so that only a small number is present, forming a "bar" across the eye (figure 21, Chapter II). A male, having but one X-chromosome with the Bar gene, has 91 to 98 perfect facets; a female with a Bar gene in both of her X-chromosomes has but 65 to 68. But a female with a normal gene in one of her X-chromosomes, a Bar gene in the other, has about 360 normal facets.

Another condition of this Bar gene has been found that reduces the number of perfect facets less; this is known as the infra-Bar gene. A female with this gene in both of her X-chromosomes has about 348 facets; with it in but one of her chromosomes, about 716 facets. By various combinations of these and other modification of the genes, individuals may be produced, under ordinary conditions, showing the following typical numbers of perfect facets—each number corresponding to a certain condition or combination of the Bar or infra-Bar genes:

25, 36, 42, 45, 65, 73, 98, 138, 200, 348, 358, 716, 800.

All these are conditions found at ordinary temperatures. But if the temperature at which the developing animals are kept is changed, it is found that environmental differences also affect the number of perfect facets. At lower temperatures, with a given set of genes, the number of perfect facets is greater; with higher temperatures it is less. So it was found by Krafka[5] that the average number of perfect facets, for females with two Bar genes, and for males with but one Bar gene, are, at different temperatures, as follows:

Temperatures, C	15°	20°	25°	30°
Females: 2 Bar Genes	214	122	81	40
Males: 1 Bar Gene	270	161	121	74

By making other combinations of the Bar or infra-Bar genes with different temperatures, many other typical numbers of facets are produced.

Thus the number of perfect facets, like the other characteristics above mentioned, depends, under given external conditions, on the kind of genes present; in this sense it depends on heredity. But with a given type of genes present, the number depends on the environmental conditions. Change of genes and change of environment may produce the same changes in this characteristic.

The production of giants in Drosophila presents a particularly striking case of dependence both on genes and on the environment. A modified gene in the X-chromosome, near its left end, causes the animals which have no other type of X-chromosome than this to grow to nearly twice the size of ordinary Drosophilas. But this increase in size takes place only if the animals are well fed during a certain period of their larval lives. Individuals without this gene do not become giants, no matter how well fed. And individuals bearing this gene, if not well fed at the particular required period, do not grow larger than the usual flies. The giant size therefore requires for its realization a particular type of environment acting on a particular type of gene. If either condition is not fulfilled, giants are not produced.[6]

An indefinite number of other cases of this sort could be given. The difference between green plants, containing chlorophyll, and white ones, with chlorophyll undeveloped, is in some cases due to a difference in genes; so that plants may remain white, even though grown in the light. In other cases the difference is due to the fact that, although all the plants can produce chlorophyll, some have lived in the dark, others in the light. That is, to produce chlorophyll the required genes must be present, and also the plants must have light. Again, there are red and white varieties of primroses; the difference in color is inherited; it is due to gene diversities. But a certain variety produces red flowers when grown in a cool place; white flowers when grown in a warm moist region, as in a greenhouse. The difference in color is now due to different environmental conditions. The list of such cases could be made very long.

Relation of Inheritance to Environment

What do such cases show about the nature of inheritance, and of its relation to environment? That which is directly inherited, in the way that property is inherited, that which is passed bodily from parent to offspring—is the set of genes, with the accompanying cytoplasm:—certain substances in certain combinations, which under certain conditions give rise to the individual, having certain later characteristics. With the same set of genes, different environmental conditions may induce the production of diverse characteristics. And with the same environmental conditions, different genes may induce the production of diverse characteristics. The same difference in characteristics that may be produced in some cases by diversity of genes is in other cases produced by diversity of environment; this is illustrated in all the cases just described. There is then no thorough-going distinction in kind between diversities producible by gene differences, and those producible by environmental differences. Characteristics do not fall into two mutually exclusive classes, one hereditary, the other environmental. A given characteristic may be altered by changing the genes; and this is the ground on which it is called hereditary. But the same characteristic may be altered by changing the environment; and this is the ground on which it is called environmental. The genes supply one set of conditions for development, the environment another set, and there is no necessary difference in kind between them. The characteristic produced may be changed by adequate alteration of either set. From the nature of a distinctive characteristic, it is not possible to decide whether it is due to diversity of genes or to diversity of environment, since the same peculiarity may be due in different cases to either set of causes. The question as to which is the decisive factor in any given case is always one for objective determination by experimentation.

Heredity and Environment in Relation to Characteristics-in-Themselves

The words "hereditary" and "environmental" are frequently applied to characteristics in themselves, not merely to diversities between the characteristics of different individuals. Consider the application of these terms to the colors of the maize plant, to abnormal abdomen, reduplicated legs, or to particular numbers of perfect eye facets, in the fruit-fly. Are these characteristics hereditary or environmental? Obviously, in view of the facts, this question has no proper application; there is no such alternative. All these characteristics are altered by changing the genes, and this is what has caused characteristics to be called hereditary. But all are likewise altered, in similar ways, by changing the environment; and this is what has caused characteristics to be called environmental. These two terms as applied to characteristics, are not mutually exclusive categories.

Heredity and Environment in Relation to Differences between Particular Individuals

But observe that as applied to *differences between particular specified individuals,* the question whether we are dealing with hereditary or environmental matters is a pertinent one; a question to which, if the facts are known, a definite answer can be given. If two individuals of maize have the same genes, yet one is red, the other green, the *difference* is environmental; it is due to the diverse conditions under which they have lived. But if we compare the same red maize plant just considered with a green plant grown under the same conditions, the difference between these two is "hereditary"; it is due to their diverse genes. If we compare two individuals of the fruit-fly that have developed under the same conditions, yet one has the abnormal abdomen, the other not, the *difference* between them is due to their diverse genes. But if they started with the same genes, and still one has the abnormal abdomen, the other not, the *difference* is due to the environmental conditions under which they have developed.

Again, is the difference between two human individuals, one of whom has a dark complexion, the other a light one, a matter of heredity or of environment? No generally valid answer to this question can be given; it depends on the facts in the case.

The difference between individual A, with a dark complexion, and individual B, with a light complexion, may be due to an original difference in their genes; so that even though brought up under the same conditions, they will differ in complexion. But the difference between the same dark individual A and the light individual C may be due to a difference in the conditions under which they have lived; A may have been much exposed to the sun, C little.

Differences between particular individuals can then, if the facts are known, be correctly assigned to one category or the other—to the effect of diverse genes, or of diverse conditions; to heredity or to environment. But the characteristics in themselves, at least those that we have been considering, cannot be correctly assigned to one class, to the exclusion of the other.

Are There Characteristics Not Affected by the Environment?

Yet what shall we say of such characteristics as the color of the eyes, in man and in the fruit-fly? All thus far known differences in eye color are due to diversities in genes, not to diversities in environmental conditions. The same is true for many characteristics of man and of other organisms. May we therefore say that such characteristics are in themselves hereditary, and not environmental? No practical error would at the present time result from such a statement. Yet we know positively that eye color is the result of the interaction of many chemicals produced by the genes. We know that if one of these chemicals is altered, through a change in the genes, the resulting eye color is changed. It is entirely conceivable that we shall some time learn to supply from outside a chemical not supplied by the genes, thus producing an eye color that the genes themselves would not produce. Many such discoveries have already been made; hormones not supplied by the genes may be supplied from outside, as we have seen in Chapter IV. It is now possible to alter many of the characteristics of organisms that a few years ago could not be altered. These matters have been under study but a few years. Beyond doubt men will in time learn how to alter many of the characteristics that at the present time cannot be changed. The fact that a characteristic is "hereditary" (alterable through changing the genes) does not imply that a way may not be found for changing it by the operation of the environment.

A Question of Particular Fact, Not of General Principle

The great need is to displace this entire subject from the basis of general principle and *a priori* argumentation to the basis of particular fact; to the basis of actual investigation for each case. Can a particular characteristic of a certain organism be modified by altering a particular environmental condition? Can the disposition, the temper, of a child, be altered by a certain type of treatment, by training, hygienic measures, or the like, as some psychologists maintain? Such a question cannot be answered by appeal to some general biological principle, but only by finding out, by experiment, by study directed on this specific question. Many characteristics that demonstrably depend on the genes and are altered by changing genes, are likewise altered by the varying conditions to which different individuals are subjected in everyday life. Others are less readily altered, but may be changed by special measures; by the introduction of special hormones and the like. There are others that are resistant; characteristics which, if they develop at all, do not differ greatly in consequence of any now known changes of conditions. Yet the possibility remains that ways of changing these will be found; for this has often happened in the past.

What is the comparative importance, the relative role, of genes and environment in producing among organisms the diversities that we commonly observe? This question, for man and for other organisms, is taken up in the next chapter.

NOTES AND REFERENCES ON CHAPTER V

1. Page 127. For an excellent account of the vitamins and their action, see *Chemistry in Medicine* (N. Y., 1928), edited by J. Stieglitz. The same volume contains a good account of the chief hormones.

2. Page 128. See R. A. Emerson, *The Genetic Relations of Plant Colors in Maize.* Memoir 39 of the Cornell University Agricultural Experiment Station, 1921, 156 pp.

3. Page 130. For an account of the relations of abnormal abdomen to the environmental conditions, see T. H. Morgan, *The Role of the Environment in the Realization of a Sex-Linked Mendelian Character in Drosophila.* American Naturalist, Vol. 49, 1915, pp. 385–429.

4. Page 131. The account of the relation of environmental conditions and of genes to reduplicated legs is from M. A. Hoge, *The Influence of Temperature on the Development of a Mendelian Character.* Journal of Experimental Zoology, Vol. 18, pp. 241–285.

5. Page 132. See for an account of the relation of genes and of environment to the number of facets of the eye, J. Krafka, *The Effect of Temperature upon Facet Number in the Bar-eyed Mutant of Drosophila,* Journal of General Physiology, Vol. 2, 1920, pp. 409–464; and the other papers cited in Krafka's paper.

6. Page 133. On giants in the fruit-fly, see C. B. Bridges and E. Gabritschevsky, *The Giant Mutation in Drosophila melanogaster.* Zeitschrift für Induktive Abstammungslehre, Bd. 46, 1928, pp. 231–284.

VI

THE RELATIVE IMPORTANCE OF HEREDITY (GENES) AND ENVIRONMENT

WHICH is more important for the characteristics of organisms, heredity or environment? Which is more important for the characteristics of man? Which is more important for the manufacture of automobiles, the materials of which they are made or the method of manufacture? This question is like the other. No single general answer can be given to either. For good results, both fit materials and appropriate treatment of these materials are required; good genes and fit conditions for their development. From materials of a particular sort, a good machine of one kind can be made, not of another kind. A method of manufacture that will fit one type of material fails with another. Materials that are excellent for one sort of machine are poor for another; and the fittest of materials require proper handling if their possibilities are to be realized. Either poor materials or poor handling can ruin a machine or an organism. If the materials are worthless, if the individual starts with thoroughly poor genes, the method of treatment, the environment, can do little. And if the material is spoiled in the process of development, it makes little difference what it was at the beginning.

Are Differences between Individuals More Frequently Due to Diversity of Genes or to Diversity of Environment?

Yet when we have before us a particular given lot of machines, some of the differences between them are due to the diverse materials of which they are made, some to diverse methods of manufacture. And in a given set of organisms, some of the diversities are due to original differences in the genes, in the materials of which the different individuals are made; others to the different conditions under which they have developed. Peculiarities due to differences between the genes of different individuals are commonly spoken of as hereditary, the others as environmental. These distinctions apply, as before set forth, only to the differences between given individuals, not to characteristics in themselves, since the latter are always a product of the interaction of genes and environment. And it is only with relation to differences between individuals that the question of the relative importance of genes and environment is pertinent.

But with relation to such differences the question is indeed one of interest and significance. If we examine a given existing set of human beings—those of a particular school, of a particular town, of a particular country, or those of the whole world—are more of the differences between them due to diversity of genes, or to diversity of environment? Are the differences due to genes more or less important for life than those due to environment?

This is a statistical question, one to be answered only by detailed study of the particular group of individuals concerned, not by appeal to any general principle. Ideally, it would be answered by comparing each individual of the group with every other individual, determining whether the differences are in each case the result of diversity of genes or diversity of environment, and averaging the result. The answer to the question would differ for diverse organisms, for diverse groups of individuals of a particular species, and for different kinds of characteristics in the same organism.

Physical Characteristics

Precise statistical answers to this question are not available, but for some organisms and for some characteristics general statements of the obvious situation can be given. With relation to their conspicuous normal physical characteristics—form, size, color, structure, sex—different organisms differ greatly in this matter. There are species or groups in which commonly occurring environmental diversities make great differences in some or all of these features. In certain organisms, the nature of the environment determines even so fundamental a matter as whether the egg shall develop into a male or a female—with the complete transformation of structure, functions and behavior that this involves. In other species the common environmental differences have little effect; form, size, structure are very constant even under widely differing conditions. In many organisms sex appears fully determined by the chromosomal condition at the time of fertilization of the egg.

The fruit-fly Drosophila, in which the effects of altering genes are better known than in any other organism, belongs to the group in which differences in the conspicuous characteristics are due mainly to original diversities in the genes. Size, form, color, structure, sex are relatively little influenced by environmental diversities, while any or all of them are deeply affected by changes in genes. Yet even in this organism, as we have seen in Chapter V, many examples can be given of the effects of environmental changes on these matters.

In many plants, and in some of the lower groups of animals, the common conspicuous characteristics are greatly altered by the environmental conditions under which the individuals live. In many plants the form and structure of stems, roots and leaves, the entire appearance of the individual, are much affected by temperature, moisture, chemical conditions, and other common features of the environment. Extensive studies of this matter have been made. In the lower plants, the Algae, many features in the life of the organisms, the method of reproduction, the nature of the reproductive cells formed, and the like, are determined by the conditions under which they live. Studies of these things have been made by Klebs [1] and by many later investigators. Some of the lower animals—the Hydroids, certain of the Protozoa, and the like—show almost as great changes under the influence of diverse environments as do plants.

In most of the animal groups, however, the changes resulting from different environments are much less conspicuous; form, structure and color are on the whole rather uniform among the individuals of a particular species, except as diversity is produced by difference in genes. Species that are domesticated show much greater variation, as a rule, in their conspicuous characteristics, than do wild ones; but study shows that these diversities are mainly due to differences in the genes of the different sets of individuals. In wild animals conspicuous changes resulting from alterations in the genes usually cause the elimination of the individuals bearing them, so that the stock remains uniform; while under domestication conditions are less exacting and the changed individuals may live and reproduce (see Chapter XV). On the whole, in most of the higher animals, the marked differences in characteristics are matters of gene diversity rather than of environmental diversity. This is the case for cattle, sheep, dogs, guinea pigs, rabbits, and for mammals in general; also for most birds. Their great differences in color, form, structure and sex are found to be the result as a rule of original differences between the genes borne by the different individuals. Alteration of environment has relatively little effect on these characteristics, save to permit or prevent the development of the individuals bearing them.

The Situation in Man

What is the situation in man? For some of the physical characteristics of man, such as eye color, it appears obvious that most of the diversities between individuals are due to original differences in genes. No method is known of altering eye color through environmental action. For color of hair the case is similar, yet not so absolute; hair color becomes changed in later life, and the change depends to some extent on experiences undergone. Differences in color or shade of skin may be due either to differences in genes, or to differences in exposure to light. Differences in stature are certainly largely due to gene differences, but probably not exclusively so. Differences in body build—stoutness and slenderness—are often due to gene differences (Davenport[2]); in other cases to differences in mode of life. Structural abnormalities of certain kinds are usually or always due to gene peculiarities; such are extra toes or fingers, webbed hands or feet, fingers with but two joints in place of three, and the like. There are other structural abnormalities that are the result of bad environmental conditions, inadequate diet, and the like; such are bow-legs, resulting from rickets.

Differences of sex in man are the result, apparently exclusively, of difference in genes, difference in chromosomes. The female has in all her cells 23 pairs of chromosomes, plus two X's; the male has 23 pairs plus an X and a Y.

Identical Twins

For matters in which the situation is less obvious—such as the precise form of particular features, small structural details, markings on the skin—evidence is obtained from the study of the similarities and differences of identical twins, as compared with other types of twins, or of individuals that are not twins. Identical twins are individuals produced by division of a single young developing embryo. At times such a division occurs incompletely, giving origin to individuals still partly connected together; "Siamese twins" and the like. Many different stages of such division are known. In cases where the division is completed, what we call identical twins are produced; these are always of the same sex, and always resemble each other closely. In the armadillo, the single egg divides regularly into four or more identical twins that form a litter; in this animal the process of division of the single embryo has been studied in detail. The twins come originally from a single egg, but division does not occur in the single-cell condition. It is brought about after development has progressed some distance; the developing embryo splits into several.

Identical twins, thus coming from a single egg, have exactly the same set of genes; they are as it were a single individual that has been duplicated. Any other two individuals, even though of the same family, even though twins derived from different eggs, have many of their genes diverse; for no two eggs are formed with the same set of genes. Comparison of identical twins with other individuals, and particularly with twins derived from different eggs, therefore gives an opportunity of determining what resemblances and differences are due to similiarities and differences of genes. Any differences between the two members of a pair of identical twins are certainly due to some other cause than gene diversity. Characteristics that are regularly alike in identical twins, but commonly diverse in individuals not identical twins, owe their similarity to identity of genes, their diversity to difference in genes.

Extensive study of identical and other twins has recently been made from this point of view (see the list of papers and books at the end of this chapter).[3] Such study has shown that there is a class of diversities between individuals that are not due to difference of genes; and not due to environmental diversities, as such are commonly understood. For not infrequently one member of a pair of identical twins is right-handed, the other left-handed; this occurs more frequently than it does in twins derived from different eggs. It is known that in individuals not identical twins, the difference between right-handedness and left-handedness may be due to a difference in genes. But the two identical twins have the same set of genes; therefore the difference cannot here be due to that cause. It appears that one of the twins must show the same "handedness" (right or left) that would have existed if there had been no division, while the other has in some way had this symmetry changed by the process of division into two. With the same genes, therefore, one individual may be right-handed, the other left-handed, depending on something that happens during early development. It is also true that very frequently one of the twins is stronger and more active than the other, usually taking the lead. This too is the result in some way of the process of division. It is suspected that the individual derived from the half that retains the original symmetry is the stronger and more active. But whatever the cause it is clear that individuals with the same genes may differ in this very important respect, depending upon something that happened during early development.

Aside from these features, the members of a pair of identical twins show remarkable resemblance in details. They are always of the same sex. They agree precisely in eye color and skin color, in the color and texture of the hair and in the form of the individual hairs. They show a great resemblance, though at times with slight differences, in freckles; in the appearance of blood in the skin; in the shape, size and arrangement of the teeth; in form and size of facial features, of ears and hands; in body build; in their illnesses and abnormalities; in tones of voice, gestures, and peculiar mannerisms. Further, there is a close resemblance in the microscopic character of the fine papillary ridges of the fingers and the palms of the hands and feet. And there is a striking resemblance in the patterns of these ridges of the palms and fingers. Here however there is a peculiar fact, resulting again in some way from the process of division. The patterns on one hand of one twin resemble those on one hand of the other twin more than they resemble those of the other hand of the same twin. At times the right hand of one twin corresponds precisely to the right of the other; in other cases, to the left of the other.

In all these features individuals that are not twins, though they may belong to the same family, or that are twins not derived from the same egg, show much greater differences than do the identical twins. It is clear therefore that resemblances in all these respects may be brought about by likeness of genes, and that diversities in all these respects are often due to diversity of genes. It does not follow of course that differences in these respects may not be induced in other ways. For though identical twins are usually alike in skin color, it is known that diversities in skin color are readily induced by differences in the environment; and the same may be true for other characteristics. The evidence from the identical twins themselves shows that with the same genes individuals may differ in right- or left-handedness; in strength and leadership; in the patterns of the ridges of fingers and palms. Nevertheless the evidence from the identical twins demonstrates that most of the observed resemblances and differences in all the features above enumerated—in form, proportion, color and structure of parts of the body—are due to similarities and diversities in the sets of genes borne by the different individuals.

Physiological Characteristics

Some of the physiological peculiarities of different human beings are known to depend upon gene differences rather than environmental differences. Some individuals lack certain materials necessary for the coagulation of the blood; so that if they are wounded, they usually bleed to death. This lack is the result of defect in a gene of the X-chromosome, since it is inherited in the typical sex-linked manner. A number of types (usually four) of blood differing with respect to their chemical peculiarities are recognized in man; these diverse "blood groups" result from diversities in genes, since they are inherited in Mendelian fashion. There are strong indications that many differences between individuals in respect to their glands of internal secretion, and in the functional action of these secretions, are due to gene differences, for peculiarities in these matters "run in families." Such differences in internal secretions bring about great diversities in temperament and behavior, so that the latter also depend on genes; a matter to which we return in the next chapter. Physiological peculiarities present much greater difficulties for genetic investigation than do structural features, so that knowledge of these relations is relatively little advanced. There is reason to believe that with increase of knowledge the dependence of physiological functions on gene differences will become more and more evident.

Diseases

Many peculiarities of human individuals are the result of a particular kind of environment acting upon a particular type of gene; the situation being similar to that described in Chapter V for certain characteristics of maize and of the fruit-fly. This is particularly true for diseases, for pathological conditions of various kinds. On these matters there has been much misunderstanding, in consequence of the common fallacy that if a characteristic is affected by the environment it cannot be hereditary; that if it is hereditary, it cannot be influenced by the environment; in other words, that characteristics fall into two mutually exclusive groups in respect to these matters. Most diseases are greatly influenced by the conditions of life; yet most or all of them are likewise influenced by the nature of the individual's genetic constitution. For the occurrence of tuberculosis, infection with the tubercle bacillus is required; and this is not a matter of genes, of heredity. But some combinations of genes yield a much better culture medium for the tubercle bacillus than do others. A person that has such a gene combination is much more likely to develop tuberculosis than another whose genes do not yield a good culture medium for the bacillus. A "hereditary" element is therefore involved. Yet the individual whose genes produce a body that is prone to tuberculosis need not develop the disease if he takes measures to prevent the bacillus from getting a foothold in his body. Doubtless there are many different types and grades of individuals with respect to this matter. Some offer a particularly favorable ground for the growth of the tubercle bacillus; others a less favorable ground, and so on through a series of grades, till we reach individuals that are almost or quite immune to attacks of the disease. The genetic constitution is therefore of much importance in connection with tuberculosis. Yet the environment is probably even more important. It is entirely conceivable that by the discovery of measures effective in preventing the transmission and development of the bacillus, tuberculosis could be brought to disappear; so that genetic differences in susceptibility to it would be of no farther consequence.

Similarly, some combinations of genes yield bodies that are much more prone than others to break out into that unregulated growth that is called cancer. In rats and mice, under the usual conditions of existence, individuals having certain sets of genes almost invariably develop cancer, while those with other genes do not. In other strains, with another set of genes, about half the individuals develop cancer; in still other strains, none. These differences are inherited in Mendelian fashion, showing that they are due to differences in one or two genes.

There are in these animals strains in which a bit of grafted cancer tissue regularly develops into a cancer; others in which this almost never occurs. There are strains that are particularly susceptible to one kind of cancer, not to another. Many grades and qualities of susceptibility exist, up to that of individuals derived from such combinations of genes that they almost never develop cancer.

It is probable that in man there are similar diversities in susceptibility to cancer, resulting from the different genes of different individuals. There is however no indication that there exist in man strains having the extreme susceptibility to cancer shown by certain races of mice. These extremely susceptible races of mice are isolated and multiplied by careful selection and by breeding in such a way as to bring together and preserve the gene combinations that are most susceptible to cancer. This does not occur in man, so that there is no reason to suppose that there are any human beings who are predestined to develop cancer, whatever the conditions. The environmental conditions that play a part in cancer are little known; though it is known for rats and mice that under certain conditions cancer is produced in individuals that under other conditions would not suffer from it. It is conceivable that knowledge and control of the environmental factors for cancer (as for tuberculosis) should progress to such an extent that the genetic factors would, in the case of man, become of little importance.

A situation that is similar in principle to that sketched for tuberculosis and cancer exists for most, if not all, diseases, infectious or otherwise. Certain environmental conditions are required for the occurrence of the disease; or at least greatly influence it. But under conditions favoring the disease, some combinations of genes yield to it, others do not. It is probable that there is no disease whatever, acute or chronic, infectious or non-infectious, whose occurrence is not influenced by the nature of the individual's genetic constitution. There can be little doubt that, other things being equal, some genetic constitutions are more readily attacked by plague, by smallpox, by typhoid, by pneumonia, than others; just as some combinations of genes yield more readily to extremes of temperature, to exposure to the elements or to unfit food; just as some gene combinations are more likely than others to come off victorious in a struggle with a wildcat, or to survive a bite from a rattlesnake.

There is a common impression that a disease or defect that is "hereditary" is inevitable, inescapable; that it is a fate against which the individual cannot struggle. The matters just discussed illustrate the fact that even though a hereditary or genetic basis exists for a defect or a disease, that defect or disease need not actually come into existence. Heredity, inheritance, has no such absolute significance as that notion implies. What the individual inherits is a constitution that under certain conditions will produce the disease; under others it may not.

Diversities Resulting from Past Environment

In all these matters of resistance to the conditions that produce disease, or to other unfavorable conditions, there is a further complication resulting from the fact that the constitution of the organism becomes altered by the conditions through which it passes. Through having undergone a mild attack of smallpox or through vaccination, the individual develops immunity to that disease. Through exposure to extremes of temperature, resistance to such extremes is acquired. Thus of three individuals who do not succumb in an epidemic, one may be immune because of his original genetic constitution; another because of the changes in his constitution induced by a previous attack of the disease, or by an immunizing agent; a third because he has prevented himself from becoming infected. The same result is produced, in different cases, by a peculiarity of the genetic constitution, by a lasting effect of past environmental conditions, and by present environmental conditions.

The relative role which each of these factors plays will be found diverse for different diseases, and diverse for the same disease under different conditions. In a population in which all are equally exposed to infection with tuberculosis, the different fate of the individuals seemingly depends mainly on their constitutional differences, genetic or acquired. But if there are great differences in exposure to infection, and in conditions favoring the disease, these become the main factors determining who shall or shall not be tuberculous. In an outbreak of typhoid fever, the different fate of the individuals formerly depended mainly on whether they became infected or not; now it depends perhaps equally on whether their resistance to the disease has been increased by vaccination; in both cases original genetic differences seem to play relatively little part.

The role of present conditions in determining the occurrence of diseases has of course always been one of the chief concerns of medical science. The alteration of the resistance of the organism through its subjection to the disease itself, or to other conditions, is now one of the chief concerns of that science. The influence of the original genetic constitution has been less studied, but has been clearly demonstrated from many diseases. For a summary of the present state of knowledge on this latter phase of the subject, the books of Julius Bauer and of Baur, Fischer and Lenz may be consulted.[4]

But the characteristics that are of chief importance for human beings are not the physical features of the body, nor even those shown in resistance or susceptibility to unfavorable conditions. They are rather the characteristics that show themselves in behavior; they are the mental characteristics. What are the relative roles of genes and environment in relation to mental characteristics? This question we take up in the next chapter.

NOTES AND REFERENCES ON CHAPTER VI

1. Page 141. See G. Klebs, *Ueber Probleme der Entwicklung. III.* Biologisches Centralblatt, Bd. 24, 1904, pp. 449–455; 481–501.

2. Page 143. See C. B. Davenport, *Body Build and its Inheritance.* Publication No. 329 of the Carnegie Institution of Washington, 1923, 176 pp.

3. Page 144. On identical twins, See H. H. Newman, *The Biology of Twins*, Chicago, 1917, 186 pp.; also by the same author, *Studies of Human Twins,* Biological Bulletin, Vol. 55, 1928, pp. 283–315; and *Mental and Physical Traits of Identical Twins Reared Apart*, Journal of Heredity, Vol. 20, 1929, pp. 49–64. See also many recent articles on this subject in the Journal of Heredity.

4. Page 150. See Julius Bauer, *Die Konstitutionelle Disposition zu Inneren Krankheiten,* Berlin, 1917; and E. Baur, E. Fischer und F. Lenz, *Grundriss der menschlichen Erblichkeitslehre und Rassenhygiene,* Zweite Auflage, München, 1923, 2 vols.

VII

GENES AND ENVIRONMENT IN RELATION TO THE MIND

Does Genetic Constitution Have a Role in Determining Mental Characteristics?

Of overwhelming importance in man are the characteristics that manifest themselves in behavior, the characteristics commonly spoken of as mental and temperamental. On these mainly depend the career for which the individual is fitted, his success or failure, the manifestations of social life, the progress of science and the arts, the type of civilization presented by any set of human beings. What is the relative role of genetic constitution and environment in the great differences to be observed in mental characteristics, in behavior? What part do genes and environment play in temper, temperament, character, conduct, in artistic, scientific, literary or technical attainments; in the accomplishment of the work of humanity?

Skepticism is at times voiced as to any role of genes, of heredity, in respect to these matters. Proponents of extreme Behaviorism expressly deny any role of heredity in these most important of human characteristics, at least so far as "normal" individuals are concerned. "We do not inherit our character, temperament and special abilities. They are forced upon us by our parents," says Watson. Many biologists on the other hand attribute to genes the preponderating role in mental characteristics.

What is the state of knowledge on this question? Here we must look first at the more general question of the applicability of the modern knowledge of genetics to man, for at times any such applicability is challenged. If diversity of genes has no role in relation to any of the characteristics of man, we may dismiss the question as to its role in mental life. If, on the other hand gene diversities affect the structure and physiology of man, it would be strange if they had no effect on his behavior, his mentality. In our earlier chapters we have freely used the characteristics of man, including mental characteristics, for illustrating the action of genes. Where lies the just conclusion in respect to these matters?

Is the Modern Knowledge of Genetics Applicable to Man?

The most general result of the experimental science of genetics is to show that the characteristics of organisms depend on the materials, the genes, which they receive from their parents, in the sense that by changing the genes with which the individuals start, their characteristics are changed. This dependence of characteristics on the materials received from the parents constitutes heredity or inheritance. The justifiable content of the statement that a characteristic is hereditary is that this characteristic can be altered by changing genes, by substituting one gene for another. It does not imply that the same characteristic cannot also be changed in other ways. Whoever reads into it such an implication falls into demonstrated fallacy, for many characteristics are known that are altered by changing genes, and so are inherited in the Mendelian or sex-linked manner, yet are equally altered by changing environmental conditions. The preceding chapters have given many examples of such characteristics.

The fundamental questions as to the role of heredity in human traits therefore are these: Can human traits be altered by changing the materials received from the parents; by changing the materials from which the individual develops; by altering the genes? And what kind of changes can be made in this way? Are there differences in human traits, and particularly in mental traits, that are commonly the result of diversity of genes?

Experimental genetics has methods of determining whether characteristics can be changed by altering the genes. It has discovered the genetic system of paired genes, with the method according to which these genes are distributed from parent to offspring. As a consequence of this method of distribution, characteristics that depend on genes show Mendelian inheritance or sex-linked inheritance (the details of the relation of these methods of inheritance to the genes have been given in Chapter II). Whenever and wherever Mendelian or sex-linked inheritance occurs, we know that the differences between the characteristics so inherited result from differences between the genes of the parents. We have therefore a test for the dependence of characteristics on genes, or as it is commonly put, on heredity.

Man has the same genetic system, operating in the same manner, as have other higher organisms. He has the same type of paired chromosomes, the same type of paired genes. The number of chromosomes in man is 48, forming 24 pairs (see figure 45). As in other organisms, the genes are so distributed to the offspring as to yield Mendelian inheritance and sex-linked inheritance; for numerous characteristics of man are known that are inherited in these two ways. Many of these have been mentioned in earlier chapters.

By using the tests of sex-linked and Mendelian inheritance, it has been found in other organisms than man that all kinds of characteristics depend on the genes, in the sense that they are altered if the genes are changed. Structural characteristics, large and small, physiological and chemical characteristics of all types; sensory characteristics, temperamental characteristics, reactions to stimuli, behavior—all classes are found to depend experimentally on genes. It can be safely said that there is no type of characteristics in which individuals may differ that has not been found to depend on genes. But remember what this means! It means simply that if the genes are changed, the characteristics are changed; it means that by adequately altering the materials of which the individuals are made, any of their characteristics may be altered. There is nothing surprising in this; it would be most surprising if it were not true. It would be surprising if by altering the materials of which an automobile is made, any and every feature of the machine and its performance could not be altered; and for an organism the situation is a parallel one.

For many of the characteristics of man, as we have seen, there is no doubt of the applicability of modern genetic science; they are inherited in the same way as are the characteristics of other organisms; they are altered by change of genes. Are there other human characteristics that are not altered by changing genes? And particularly, is this true of mental characteristics? Are mental characteristics independent of the constitution and physiology that are so deeply altered by change of genes? Or do diversities of genes indeed result in differences in the characteristics shown in human behavior?

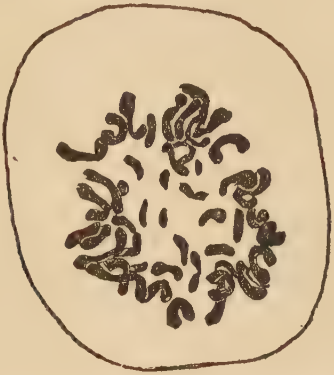


Figure 45—the 48 chromosomes of man, after Painter. The figure shows the chromosomes in a cell of a white man,

Are Mental Differences Produced by Diversity of Genes? By Diversity of Environment?

Turning to direct experimental evidence, in other organisms the characteristics shown in behavior are indeed altered by changing genes. In the fruit-fly Drosophila the reaction toward light depends on a gene in the X-chromosome, located at the point 27.5 on the chromosome map. When that gene (known as "tan") has a certain constitution, the individuals bearing it fly toward a source of light coming from any direction; they show "positive phototaxis." If that gene is constituted in another way, the individuals bearing it do not fly toward a source of light. These two diverse methods of behavior show sex-linked inheritance: if fathers that fly toward the light are mated with mothers that do not, all the resulting daughters fly toward the light, all the sons do not.

Many sensory peculiarities in animals are similarly known to depend on the genes, since they show Mendelian or sex-linked inheritance. The dispositions that we call wildness and tameness are likewise, by the same test, shown in certain animals to depend on the genes.

Coming to man, certain sensory characteristics are well known to depend on genes. One is color-blindness; for it shows in some cases sex-linked inheritance—demonstrating that some of the genes that affect color vision are in the X-chromosome. By the same token, normal color vision depends on genes; for when mated with color-blindness, normal color vision is inherited as a sex-linked dominant. Sharpness and dullness of vision are similarly shown to depend on genes. So also do deafness and normal hearing; for they also are frequently inherited in Mendelian fashion.

Again, in man the general efficiency of the brain, of the mind, is known to depend on genes, for alteration of a single gene may produce feeblemindedness. We know this, because feeblemindedness is often inherited according to the simple Mendelian system, which results when father and mother differ in a single gene affecting the characteristic considered. And feeblemindedness exists in many grades of intensity or diversifications of kind, corresponding to many diverse conditions in genes.

"Normality" of mind of course also depends on the condition of certain genes, since when a normal and a feebleminded person are mated, the normality as well as the feeblemindedness is inherited in the Mendelian manner.

What all this means, if we compare inheritance here with what we know of inheritance in cases more fully studied, if we compare it with the inheritance of such a characteristic as the eye color of Drosophila, is that the interaction of many genes, and doubtless of many other things, is required to build up a normal brain, a normal mind. If any one of these fundamentally necessary genes is seriously defective, the brain and mind are defective; if they are altered, the brain and mind are altered.

Besides evidence based upon actual observation of Mendelian and sex-linked inheritance (as shown by the ratios of different types of descendants produced), dependence of characteristics on genes is shown by the repeated appearance of a characteristic among the members of a family, or among close relatives, when there are not differential environmental causes for such appearance. Such evidence is less direct than that based on the observation of typical inheritance ratios, but taken in connection with the occurrence of these ratios in the same organisms it is often conclusive, and in many cases it has led to the later observation of the typical ratios. On this basis there is strong evidence that proneness to certain types of insanity depends upon certain genes borne by the individuals of particular families, since such insanity "runs in" these families. This of course does not mean that the individuals bearing these genes must necessarily become insane, but only that they may become insane under conditions in which individuals with other genes would remain sane.

We know further that such matters as dullness, stupidity, and their opposites, various diversities of temperament, and the like, depend on the genes. For they are known to depend on the nature, quality and quantity of certain of the internal secretions or hormones; and these latter in turn depend on the genes. Examples of this dependence have been given in Chapter IV; notably the dependence of mentality on thyroid secretion. Individuals whose genes produce a thyroid that fails to function in the normal way never fully develop mentally; they remain cretins, imbeciles. By introduction of thyroid from outside, replacing what the genes have failed to produce, the individual is caused to develop into a normally intelligent person. There are many ways in which temperament and mentality depend on the diverse internal secretions; and these latter are known to depend on the nature of the genes, being diverse with differences in genes. In these matters the dependence of mentality on genes is of course indirect. But the dependence of all developed structures and functions on genes is indirect, in the sense that all have passed through many developmental transformations, in all of which the genes play a part. The relation of mental characteristics to genes is in this respect the same as that of other characteristics.

It is beyond question therefore that mental characteristics depend on genes, in the sense that they are altered by substituting one gene for another. This does not in the least imply that mental characteristics do not also depend on environmental conditions, in the sense that they may be altered by environmental conditions. The performance of an automobile depends on the materials of which it is made; but also on the conditions, the treatment, to which those materials have been subjected. There is a similar situation for the behavior of man.

There remains then the question of the relative role of gene differences and environmental differences, in mental characteristics. What sort of mental diversities are made by each? Which are the more frequent and the more important for human life?

An organism's behavior is his system of reactions to stimuli; it is his system of adjustment to the conditions (present, past or future) that he meets. This system, viewed as it were from the inside, is what we call the mind. The details of the reactions of course depend on the stimuli, the conditions, that are met. The fact of the great role of environment in behavior and mentality cannot be called in question. No one will be found to maintain the absurd paradox that behavior has no relation to the conditions met in life. The individual behaves differently in the presence of food and in its absence; and this is but an example of a relation met everywhere. In an infinite number of details the behavior of the individual depends on the conditions confronting him at the moment of reaction.

How then can genes influence this behavior? Obviously, not through making behavior independent of the conditions, but by causing different individuals to behave diversely under the same conditions. And this of course we observe. One individual reacts to one element of a situation, another to other elements, a third not at all. In some the reaction is to the integrated situation as a whole, in others to only certain features of it. One individual reacts hastily and ineffectively, another slowly and effectively, a third rapidly and effectively. Some behave prudently and with foresight, others are imprudent and shortsighted. Some behave with "tact," others without it; some with dignity, others without it; and so on through an infinite series of differences.

Have the genes a role in bringing about such diversities of behavior? Here again we meet a great difficulty, the same difficulty met in dealing with the role of genes and environment in resistance to unfavorable conditions; but here the difficulty is multiplied many times. The experiences through which the individuals pass, the conditions that they meet in development, alter them, change their reactions to present conditions. Such alterations are brought about in manifold ways. An individual that has recently eaten behaves diversely from one that is hungry; a fatigued individual from one that is rested. A person that has had a strong emotional shock behaves differently in consequence; and there are infinite grades and qualities of such emotional experiences modifying later behavior. An individual that has learned something (whatever the nature of that process) behaves thereafter differently in certain respects from one that has not learned this particular thing. And the number and variety of things that can be learned, and that correspondingly modify behavior, is for practical purposes infinite. When all such possibilities of modification are taken together, we have before us a system of relations by which we might account, formally and logically, for almost any observed diversities of behavior. And this is what is actually done by the extreme behaviorist.[1]

But the same logical situation exists with relation to the genes. The variety of gene combinations is as great as the variety of environmental modifying factors, and they may as readily alter behavior as may the latter; unlimited possibilities are open in both directions. The question is therefore not one of possibilities and logic exclusively, but of concrete fact. Are all diversities of human behavior (under effectively the same present conditions) due to previous experiences undergone by the individuals in their development? Or are some of them due to the diverse combinations of genes, the diverse materials from which the different individuals are developed?

Nothing can be more certain than that both these sets of factors play a role. No one will deny the modification of mentality and behavior by the diverse experiences undergone by different individuals. And no one who examines the facts summarized in earlier paragraphs of this chapter, the facts as to the relation of genes to sensory characteristics, to the general efficiency of the brain, to the internal secretions that so greatly influence temperament and mentality—no one who gives these facts unprejudiced consideration and due weight will deny that diversity of genes affects mentality and behavior.

What Kinds of Mental Diversities Result from the Two Classes of Factors?

What remains then is to disentangle the effects of these two classes of factors affecting human behavior. What kinds of differences are made by diversity of genes, what kinds by diversity of past conditions? Are the two kinds diverse in type or extent; and in what ways?

The process of disentanglement is most difficult; in many respects it is impossible at the present time. For many of the observed differences between human individuals, there is no way of determining which set of factors is responsible. The psychologist, the behaviorist, the sociologist, can prove that the later behavior is altered by experiences undergone; the geneticist can prove that diversity of genes results in diversity of behavior. But for the observed present diversities in behavior between particular individuals there is often no method of deciding which is at work. For such judgments as can be formed, one must pass in review what is known as to types of differences producible on the one hand by genes, on the other by environment.

What Kinds of Mental Differences Arise from Diversity of Genes?

Diversity of genes can produce very great differences in mentality. It can produce the difference between a feebleminded individual and a normal one. It can produce the difference (under effectively the same conditions) between an insane individual and a normal one. It can produce great or slight differences in the efficiency of the senses.

Further, diversity of gene combinations brings about the differences, whatever they are, in the mentality and behavior of the two sexes. The female contains a certain set of genes in duplicate series, while the male has the same set in but a single series; from this result all the differences between the sexes, structural, physiological, mental. The same individual that develops into a female would have produced a male if one of the two X's in the fertilized egg had been removed. The diversity of behavior in the two sexes is of course mediated by complex differences in structure and physiology that arise during development, these all tracing back however to an original difference in gene combinations. In grasping the differences made by genes, one must keep in mind this typical case of diversity of sex, with all its consequences for structure, physiology, mentality, behavior.

Diversity of genes can bring about the profound or slight differences in temperament and disposition that result from differences in the internal secretions, for the latter depend on the genes. By this means it can bring about great or small differences in respect of stupidity and intelligence.

All the effects above mentioned of gene diversity on mentality and behavior are solidly established. They involve many changes, great and small.

There remains the question whether diversity of genes can bring about the differences in aptitudes, types of ability, emotional attitudes, and the like, which distinguish normal human individuals as we find them. Can diversity of genes bring about the difference between the individual that learns rapidly and readily and the one that learns slowly and ineffectively? Can it bring about the differences in grasp and understanding that so strongly mark different men? Can it bring about the difference between the individual that is readily swayed by every surrounding influence, and the one that holds his course without deviation? Can it bring about the difference between the child that is readily suggestible, tending to follow instructions, and the one that is contra-suggestible, tending to react adversely to instruction or command? Can it bring about the difference between the individual who makes satisfaction of his own immediate personal wants the mainspring of his action, and the one who acts for the interests of his companions? Can it bring about the difference between the individual of artistic tastes and habits, and the one that is without these? Can it bring about the difference between the individual that selects engineering as his occupation, and the one that becomes a laborer, a physician or a poet?

Most of these and similar questions cannot be answered by direct appeal to the demonstrative ratios characteristic of Mendelian and sex-linked inheritance, as can questions concerning the dependence of feeble-mindedness or of color-blindness on genes, or the dependence of sex differences on genes. To form an enlightened opinion on them, one must look at the general picture of the results of diversity of genes; must consider the nature of gene action, as revealed by the study of its effects on other characteristics, and in organisms on which exact breeding experiments are possible. It is positively known that gene diversities bring about great differences in mentality. Slighter differences in genes would bring about differences in mentality that are less, but still important. The dependence of these slight differences on genes it would not be possible to demonstrate directly by the observation of inheritance ratios, owing to the complicating action of environmental differences and the impossibility of carrying on controlled breeding experiments in man. All knowledge of genes shows that for every great difference in characteristics induced by them, there are hosts of lesser differences in the same characteristics that are similarly brought about. And such differences induced by diversity of genes are of many types and qualities. There is no reason why this should not be true of the brain and mentality of man. There are fifty different types of eye color induced by diversity of genes in Drosophila; is it credible that there should not be a great number of diversities so induced in a matter so complex as the brain and its functions? Reasoning thus from the general picture presented by the action of genes, it must be held that mentality and behavior are affected in a great number of different ways by the combinations of genes present in the different individuals. The actual situation as to mental diversities is of just the sort that must be expected if this is true.

When all this is taken fairly into consideration, one must conclude that gene diversities are a potent cause of mental diversities, whether slight or great; and of mental diversities not merely of some particular type but of many types. And the general picture presented by experimental genetics makes highly probable the correctness of a farther step in this direction. The indications are, as before set forth, that all characteristics of organisms, without exception, can be altered by changing the original constitutions of the individuals, by altering their genes; just as all characteristics of a machine, including its performance, may be altered by changing the materials of which it is made. There is no ground for refusing to apply this generalization to mental characteristics. The fact that such characteristics can be altered by diversities of environment has sometimes been assumed to supply a ground for denying the effectiveness of genes, but this is a fallacy. As shown in previous chapters, many characteristics that are indubitably altered by gene differences are likewise altered by environmental differences. No cogent ground can be alleged against the proposition that any mental characteristics, any feature of behavior, can be altered by a change in the genes of the individual; and all our knowledge of genetics strongly indicates that this is true.

Shall these implications of the general picture presented by genetic science be accepted? Acceptance is far more likely to lead to correct conclusions than rejection. In the remainder of the present account, therefore, these implications will be accepted; our exposition of the interactions of genetic constitution and environment will admit that any mental or temperamental characteristic may be altered by change in genes.

Accepting this, all the questions above proposed as to the kinds of changes producible by diversity of genes are to be answered in the affirmative. Any of the differences suggested may be brought about by diversity of genes. There is reason to believe that of two individuals with similar histories, one may show a better knowledge of Latin syntax in consequence of an original difference in the genes with which the two individuals began life; and the same is true for any other difference whatever in mentality or in performance. It is not that there is a special gene "for" or representing each distinguishable capability of the organism, but only that through the innumerable diversities of gene combinations, constitutions of every shade and kind of difference in capability are producible. Individuals made from diverse kinds of materials may in consequence thereof show differences in mentality of any sorts that occur.

All the individuals of a human population (except the members of pairs of identical twins) differ in their gene combinations, in most various ways. If we imagine therefore a human population all subjected throughout life to the same environment, we should still find differences in temperament, in aptitude, in ability, in morality, of perhaps all the diverse types now observed.

What Kinds of Mental Differences Arise from Diversity of Environment?

Turning now from genetic factors, what differences in mental and temperamental characteristics can be made by diversity of environment? Under diversity of environment we shall include all the different experiences that individuals may undergo from the time they are single cells, with the full complement of genes; the effects of their own actions as well as the effects of outer influences on them.

All agree that many details of the present actions of an individual depend upon his past environment, his past experiences. Ideally, this means that two persons with the same set of genes (such as a pair of identical twins), will behave differently under the same present outer conditions, depending on their past experiences. Differences in hunger and satiety, in fatigue, in habit, in knowledge, and a hundred other things resulting from past conditions, bring about diverse behavior under given conditions. Knowledge, habit, culture—these beyond question tremendously influence behavior; as to this there will be no dispute.

How great, lasting, and important are the changes in mentality, in temperament, in character, induced by environmental conditions? How far may the different types of temperament, ability, and special aptitudes, observed in human beings, be the result of the different conditions to which they have been subjected during development?

Decisive experimental answers to these questions are difficult to obtain. Individuals subjected to different environments almost invariably have also diverse combinations of genes, so that it may be impossible to decide which set of factors brings about any observed results. For an intelligent judgment on these questions, the opinions of acute observers of human nature are worthy of consideration, along with the results of professional and experimental studies on human behavior. Study of identical twins that have lived under diverse environments furnishes ideally the most satisfactory evidence on this matter, but such cases are so rare, and the diversity of environment on the whole so slight, that comparatively little has thus far been contributed by them. Before proceeding to a more general examination, however, it will be well to look at the evidence thus far obtained from this source.

Identical Twins

In identical twins we have two individuals with the same sets of genes. Any differences in their mental characteristics are therefore due to something that has happened during their development, to their diverse experiences and environment; not to diversity of genes. Four pairs of identical twins that were separated early and that lived separately, have been studied by the use of modern psychological tests; one pair by Muller, the geneticist, three by Newman, the embryologist and specialist in the biology of twinning.[2]

Muller studied twin sisters that had been separated when two weeks old, and that did not see each other until they were 18 years of age; from that time until the age of 30 they lived separately more than nine-tenths of the time. They lived, however, under similar social conditions, in the northwestern mining and ranch country, but had considerably different experiences in life. Physically they showed the extreme similarity, almost identity, in characteristics, that is common in identical twins. Both "have always been intellectually active," "both have been extremely energetic, capable and popular, and they have been prominent in all sorts of club work in their respective communities." "Both have had two or three attacks of tuberculosis, almost simultaneously." One had, and the other nearly had, a nervous breakdown in the late teens. The usual "intelligence tests" gave results very closely alike for the two twins, though quite different from the most usual scores for these tests; indicating that the resemblance was due to the similar genetic constitution of the two. But "the non-intellectual tests —of motor-reaction time, association time, 'will-temperament,' emotions and social attitudes—gave results in striking contrast with those of the intelligence tests, in that the twins made markedly different scores in all these tests." The differences were on the average greater than those between two individuals taken at random, and seemed "to be correlated with salient differences in their past experiences and habits of life." In this case therefore study of identical twins indicates that the environment and experiences of the individual have large effect on temperament, emotions and social attitudes, producing marked differences in these matters, in individuals that are genetically the same. On the other hand, such performance as is brought out by intelligence tests had been little affected by the diverse environments—which however, it is to be remembered, were in general features similar. "What the effect might have been of changing the social class, the country, or the color (were that possible) of one of them, it would be impossible to predict," says Muller.

Newman studied two pairs of twin sisters and one of twin brothers. Each of these pairs clearly consisted of identical twins; and in each case the two members were separated before they were two years old and lived apart thereafter for twenty years or more.

The first pair of twin sisters were born in London, and were separated at the age of 18 months. One lived in Ontario, Canada, the other in London. After 17 years of separation they joined each other in Ontario and had been together about a year when tested. Their environments were very different during the period of separation: "as different as one is likely ever to find in cases of separated identical twins." This pair of twins, curiously, gave differences in those tests where Muller's pair gave similarities, and gave similarities in those tests in which Muller's pair gave differences. "The twins dealt with in this paper are very different in mental capacity, the difference being three times as great as the average of fifty pairs of identical twins reared together," says Newman. On the other hand, this pair showed great similarity in their will-temperamental qualities, in their emotional reactions. In this case therefore we have strong indications that differences in the experiences undergone by the individual affect greatly his mental traits, his performance in matters brought out by intelligence tests.

The two sisters of Newman's second pair had received very different educations, one having attended school seven years longer than the other. Concerning these Newman gives the following summary: "These twins, remarkably similar after being separated at eighteen months of age and unknown to each other for nineteen years, have been profoundly modified by the very different educational careers. In every test of mental capacity, whether of so-called native ability, or of achievement, 'G,' the more highly educated twin, has distinctly the superior mind. Obviously, mental training improves the ability of an individual to score well on any sort of test, even such an one as the International Test in which no language is used and only degrees of brightness or mental alertness are supposed to be tested." "In contrast with the great difference in mental power stands the fact that in all the tests of emotional traits and of temperament, the twins give the impression of being remarkably and unusually similar."

Newman's third pair consisted of two young men, one of whom, "C" had lived mainly in the city, while the other, "O" had lived in the country. They were tested at the age of twenty three. "In native ability they seem to be nearly identical. The one outstanding difference is in their general personalities. 'C' impresses one as more dignified, more reserved, more self-contained, more unafraid, more experienced, and less friendly. He seldom smiles, has a more serious expression about the brows, eyes and mouth. He stands more erectly with chin held in and brows drawn down somewhat over his eyes. 'O' is the opposite in all of these respects. He is more the typical country boy, laughs readily, and is not on his dignity at all." Newman emphasizes that "the 'personalities' of the boys were utterly different."

Thus the study of the four cases of identical twins reared separately is favorable to the claims of those who hold that environment and experience may have a great effect on mental and on temperamental characteristics, producing marked difference in these respects, even in individuals that are genetically alike. The four cases, however, support equally the view that the genetic constitution likewise affects greatly these matters. For in all cases the twins reared under diverse environments were much more alike in certain respects—in some cases in mental processes, in others in temperament—than can be accounted for on any basis except their identity in genetic constitution. The results of the study agree thoroughly with the conclusion, practically certain on other grounds, that both the genetic constitution and the environment deeply influence mental and temperamental characteristics; and that effects produced in one case by genetic constitution may be produced in another case by environment.

Individuals That Are Not Twins

Turning to a more general consideration of the matter, the differences produced in mentality, in personality, by the experiences through which the individuals pass, are by some judges of human nature held to be profound. Shakespeare asserts that "use almost can change the stamp of nature," and on a question of human nature Shakespeare's opinion is worthy of respect. Of equal weight is the opinion of Bacon (unless one make him merely Shakespeare's *alter ego*), that "custom only doth alter and subdue nature" and that "nature nor the engagement of words are not so forcible as custom." The modern Behaviorists, led by Watson, go even beyond the opinion of Shakespeare and Bacon, holding that all differences in mentality and character among "normal" individuals are due to diversities of experiences; wherein they attribute very great effects to the experiences undergone by the infant: the shocks and sets received before the age of eighteen months. Educational practice is based largely on the belief that the human individual is deeply influenced by the conditions to which he is subject. Most movements for the reform of the individual or the amelioration of society rest on the same basis.

What are the types of changes in mentality, character, personality, that may be induced by the experiences undergone by the individual during his development? It is clear that negative changes of a most radical type can be so induced. A blow on the head may permanently reduce the most brilliant individual to idiocy. Disease may reduce vigor and render accomplishment impossible, bringing the ablest person to the level of the lowest. Defects in the apparatus of internal secretions, producible by accident or disease, must lower efficiency and alter characteristics for the worse, in many ways.

But may environmental action induce deep-lying positive changes in characteristics, changes not falling in the category of injuries, not classifiable as defects? For clearness of thought on this question, it is helpful to conceive a population, all of whose individuals have the same original constitution: the same combination of genes; individuals that have the same relation to each other as have the two members of a pair of identical twins. Populations of this sort, with vast numbers of individuals, occur in many lower organisms. Imagine first such a human population in which the gene combinations are those of some "normal" individual, of some typical capable citizen. What differences in performance, what differences in mentality and character, what differences in career, in the ultimate goal reached, will be produced by different environments acting on these originally identical individuals?

The single human individual it not a closed-in system with an impervious shell, but on the contrary is so constituted as to be capable of response and of adjustment to a great number of diverse conditions and situations. He has, not a single definite prearranged fate or tendency, but a vast number of capabilities, a vast number of keys, as it were, through which the environment may play upon him; a multitude of impulses, tendencies toward action in diverse directions. Each of these is as native, as original, as any other. On the conditions met depends which of these impulses will be carried out. And the carrying out of any impulse alters the constitution of the individual, giving him a "set" in a certain direction, so that his reaction to many or all future conditions is altered. Thus an early set, under the influence of a certain condition, may decide the main features of the later career. Different members of the originally uniform population meeting thus different influences at an early stage, progress in different directions, through diverse careers, to different goals. Each human individual has the possibility of many diverse careers; as the young individual of Amblystoma has the possibility of an adult career either as a water dweller adjusted to an aquatic life (axolotl) or as a land dweller adjusted to a land life (Amblystoma). Only one of the many diverse careers can be realized by a given individual; which one this shall be depends on conditions met in the development of that individual.

Of such a population of genetically uniform individuals, Watson's dictum in his *Behaviorism* may well be true:

"Give me a dozen healthy infants, well formed, and my own specified world to bring them up in and I'll guarantee to take any one at random and train him to become any type of specialist I might select—doctor, lawyer, artist, merchant, chief and, yes, even beggar-man and thief, regardless of his talents, peculiarities, tendencies, abilities, vocations, and race of his ancestors" (Behaviorism, p. 82).

Any one of the originally identical individuals of our imagined population has the capability of carrying through any of these careers, which one shall be realized depending on the influences brought to bear on him during his lifetime. (The same may be true, as Watson holds, for the "normal" individuals of an actually existing population, though differing greatly in their genes—although the individuals will differ much in their efficiency in the different careers, as set forth later.) Such a population, identical as to genes in all its components, would realize the situation postulated by Watson: all diversities due to environmental differences, none to genetic differences.

But in what characteristics, aside from the outer diversities of circumstance and accomplishment, would the individuals of this genetically uniform population differ? What kinds of diversities in mentality, character, personality would be observable as results of diverse experiences of the individuals? Pass in review certain of the kinds of possible mental differences between human beings:—

Can diversity of environment bring about differences in temper and temperament? Can it induce in one individual a sanguine, a cheerful disposition, in another a pessimistic, a melancholy one? Can it make one individual "good-natured," another irritable, ill-natured, savage, in disposition?

Behaviorists, educators, religious teachers, reformers, many professional students of human nature, urge that such effects can indeed be produced; they point to what they hold to be instances of such effects. The certainty that their interpretation is correct is diminished by the fact that they are dealing not with a genetically uniform population of the sort we have imagined, but with a population whose individuals differ greatly in their original constitutions, so that it is difficult to disentangle the effects of diverse gene combinations from the effects of diverse environments. Yet as seen on a previous page, study of identical twins, as far as it has gone, supports the conclusion that marked temperamental differences are producible by diversity of environment. And certainly there is nothing in the results of experimental genetics that negatives such a conclusion. Environmental diversities as certainly affect the characteristics of organisms as do genetic diversities; what particular set of characteristics is affected, and how much, in any given organism, is to be determined solely by empirical study, not from general principles. Environmental diversities greatly affect the activity of the organs of internal secretion; changes in these might well deeply affect temperament and disposition, just as a change in genes might affect them.

Can diversity of environmental influences bring about the commonly observed difference between the child that docilely follows suggestion, instruction and command, and the one that tends to react adversely to these things; between the suggestible and the contra-suggestible individual? Can it bring about the difference between the individual who makes satisfaction of his private personal wants the mainspring of action, and the one who acts for the interests of others; between the selfish and unselfish individual? The geneticist may feel, perhaps correctly, that such differences are usually due to an original diversity of constitution; but the question remains, can they also be brought about by diversity of environmental influence? The behaviorist, along with other students of human nature, asserts that they can and are. The question is purely one for objective evidence, one of experimental fact; there is nothing in genetics that makes possible an *a priori* answer.

Can diversity of environmental influences bring about differences in special aptitudes and abilities? Can it bring about the difference between the individual with artistic ability and the individual without it? Can it bring about the difference between the sensitive and creative musician and the person who has no taste for music, no appreciation of it? Can it bring about the difference between the child that inclines to a literary career, another that evinces special ability in mathematics, and a third whose inclinations are only to sensual enjoyments, to the exclusion of all intellectual pursuits? In a population all of whose members were identical in genetic constitution, would such differences occur? This question may give pause to many persons that are otherwise disposed to admit the very great influence of the environment. Yet beyond question there are individuals in whom the elements are so mixed that they have a potential love for art, engineering, mathematics, sensual enjoyments, and many other things; in such individuals the environmental influences will determine which of these shall come to fruition. On the other hand, it appears that there are individuals in whom the capabilities for some of these lines of activity are nearly or quite lacking, so that no environment can make of them great musicians, great mathematicians, great engineers.

Next a fundamental question, one that goes to the heart of the relation between genetic and environmental influences: Is the difference between individuals in their ability to adjust to environmental conditions itself under the influence of the environment? Can diversity of environment bring about the difference between individuals that are responsive to environmental influences and those that are not, those that adapt themselves little or ill to circumstances? Can it bring about the difference between those that learn readily, rapidly, and much, and those that learn slowly, and but little? Can such differences be brought about by differences in education, in training, in experience? Is it true that, as Dewey [3] expresses it, "in learning habits, it is possible for man to learn the habit of learning"?

There will scarcely be dissent from the statement that there are great and numerous original differences, genetic differences, between existing individuals in their powers of adjusting to the environment, their powers of learning. But this does not dispose of the question whether in a given individual these powers may be decreased or increased, depending on the experiences through which he passes; whether therefore individuals of the same genetic constitution may not in a later period of life show differences in these powers. Here again, the science of genetics raises no presumption that this cannot occur; it is purely a matter for empirical determination. Students of human nature on the whole agree, apparently, in holding that the power of learning may, in human beings, be altered, increased by proper treatment. This is entirely compatible with the further opinion, held by many, that existing differences between individuals in these respects are in the majority of cases native, the result of differences in gene combinations—a matter for later discussion. Further, if there exists capability for increase in the power of learning, this capability itself will vary in individuals of diverse original constitutions, being slight in the "stupid" individuals, and increasing as the gene combinations become more favorable.

Interplay of Genes and Environment

We have conceived of a genetically uniform population, all of whose members have a gene combination as favorable as that of a normal capable citizen. Conceive now of a genetically uniform population having a poor combination of genes, so that it is of distinctly low grade; so that it is composed of the type of individuals that we call dull. In such a population the effects of environmental diversities will be much less than in a genetically superior group. Dull people are those little affected by environment; in deciding their fate, genes are more powerful than environment. Since it is the very quality of their gene combination that it does not adjust well to environmental differences, little can be done to help the stupid. "Against stupidity the gods themselves do strive in vain," says Carlyle. "Though thou shouldst bray a fool in a mortar—with a pestle, yet will not his folly depart from him," says the author of the book of Proverbs. Yet even for some types of stupidity modern developments of biological science hold out hopes. As we have seen elsewhere, the cretin, whose genes do not produce a thyroid secretion of adequate quality and quantity, is a miserable idiot. But by supplying him artificially with the thyroid secretion that he fails to produce, he may be converted into a normal human being, responsive to the variations in his environments and adjusting himself to them. How far this sort of thing may go in the future no one can predict. By supplying from the outside the hormones or other chemicals that the individual's own gene combination do not provide, possibly other classes of the dull and irrational will be made capable and intelligent. Yet it is an immeasurably better plan for our own genes to supply us with the inner conditions for becoming efficient and intelligent; for even though for the individual's own life his gene differences are remedied, he still passes on his defective genes to offspring.

In general it is true that diverse organisms differ greatly in their capabilities of adjustment to diversities of environment. The "mind" of the worm adjusts to a most limited range of environmental conditions; the mind of the guinea pig to a somewhat greater range. The cat and dog (each within his characteristic range) may adjust to a rather complex and diversified set of conditions. In man the capability of adjustment is much greater than in any other organism. But among different human beings, in consequence of diversities in their genetic combinations, the degree and delicacy of adjustment varies greatly. The dull person is one whose system of adjustment works poorly, without delicacy and discrimination. In a population composed of genetically dull persons, much less diversification of character and personality would result from environmental differences than in a population of genetically superior individuals. A society of genetically poor individuals will yield a dull civilization, without versatility, without strongly marked differentiations.

If one conceives of a population composed of two sets of individuals genetically diverse, one set little responsive to environmental differences, the other extremely responsive, one makes an approach to a correct conception of an actually existing human population. To make a closer approach, one must very greatly increase the number of genetically diverse classes. And these diverse classes differ genetically, not merely in degree, but in their special aptitudes, some tending more readily to one type of activity, others to other types, some responding in one manner to a certain type of environment, others in a different manner. Carry this genetic subdivision to its logical extreme, so that every individual represents a diverse class of genetic combination (save for the cases of identical twins), and one has the condition found in an existing human population. Upon this set of diverse individuals, each reacting somewhat differently to given environmental conditions, allow the extremely varied conditions of human life to act; the result is what we see before us in a human civilization.

In the mental characteristics of such a human society we find the ultimate flowering of the system of action that we have before seen at work in the colors of plants (Chapter V), and in the production of immunity and resistance (Chapter VI). The same kinds of differences between individuals can be produced by diversity of genes and by diversity of environment. Many of the diversities that we observe are due to one of these causes, many to the other. There are few if any types of mental diversity that can be asserted on *a priori* grounds to be certainly genetic or certainly environmental. To determine to which category a given diversity belongs requires a knowledge of the pertinent concrete facts for the particular case examined.

Even in respect to diversities in concrete knowledge, or in skill in particular arts or trades, although these appear at first view to be exclusively matters of instruction, training and experience, diversities of genetic constitution have a role. A difference between two individuals consisting in the fact that one can speak French while the other cannot, or in the fact that one can play the piano while the other cannot, results in many cases from the different instruction, training, or other experience undergone by the two. Yet two individuals with the same amount of training in the same line often show great differences in their attainments of knowledge and skill, in consequence of an original diversity in genetic constitution. In such matters the results of differences in genetic constitution and in environment become inextricably blended. Two individuals are given the same opportunities for the acquirement of knowledge or skill; for learning French or playing the piano. In consequence of genetic diversities, one takes advantage of his opportunities, the other does not; one subjects himself to the experiences necessary for acquiring knowledge or skill in these matters, the other does not. The consequent differences are due immediately to the different experiences undergone; mediately to the genetic differences that led to the diversity of experience. A great number of the differences between human beings living under the same system of culture are of this character. Genetic differences intervene continually to produce diversities of environment and experience, resulting in differences in characteristics.

For individuals living under different cultures or at different eras of history, the differences in concrete knowledge and skill are of course more nearly exclusively the result of environmental diversities. No one could speak French before the French language came into existence; no one can play the piano when or where pianos are unknown. The diversities thus resulting from differences in the general state of culture to which individuals are subjected are very great; their extreme importance seems at times to be neglected by geneticists. The very great differences between the people of the twentieth century A. D. and their ancestors of the twentieth century B. C. are, so far as can be judged, not at all matters of genetic constitution, for there is no indication of a significant change in the genetic constitution of the human stocks in this period. Whether for better or worse, the diversities between the civilization of the present time and the ancestral barbarism of ten thousand years ago is a matter of environment, not of genetic constitution. Any cultural differences as great as these, existing now in diverse quarters of the earth, may then be similarly due to environmental causes, and be alterable without alteration of the genetic constitution of the stock. Whether this is the case, or whether genetic differences are largely responsible, can be determined only by study directed precisely on this question; perhaps only through later examination by future historians of what shall occur as centuries pass.

The same considerations apply to proposed changes in the civilizations and social systems of the present time. A given civilization is the outgrowth of the interaction of the genetic constitutions present in the population, with the environment —including knowledge, inventions, traditions—of that population. By changes in the latter set of factors enormous differences have in the past been made in the cultural system. By farther changes in these environmental factors, equally great changes in the cultural system may in the future be brought about. No cultural system is the outgrowth of genetic constitution alone. No predictions as to the possibility or impossibility of such proposals as the enforcement of prohibition or the suppression of war can be reliably predicated on the constancy of human nature; for with the same human nature diversities of the most radical character in customs and culture are compatible and have occurred.

In a human population of a given era and a given country—as for example in the United States at the present time—we have then a great number of genetically different classes of individuals, diverse in their capabilities, their tastes, their tendencies to action. All of these, so far as they do not fall in the distinctly defective groups, have marked capabilities of adjustment to different conditions. It follows then, that by subjection to adequately diverse environments, diverse training and instruction, any of them can be made, as Watson asserts, into "doctor, lawyer, merchant, chief," or made to take various other places in society. Biology has no proper quarrel with such an assertion. Limiting it to "normal" individuals, Watson simply excludes by definition all genetic classes that have not capabilities of adjustment sufficient to justify the assertion. Though biology can take no exception to this positive statement of the remarkable power of adjustment of individuals to diverse conditions, it must emphatically dissent from the negative conclusion drawn from it—namely, that heredity has nothing to do with the diverse aptitudes, temperaments and fates of individuals. What an enlightened view of biology would add to Watson's statement of the case is this: While any of the normal individuals, taken early and properly guided, could be made into physicians, it would take different treatment to accomplish that end in the different individuals. And some would make but poor sticks in that profession, at the best, while others would become Mitchells, Oslers or Welches. It is no news, as Cattell has remarked, that very unfit persons may be made into physicians. By making certain individuals into lawyers, good merchants would be spoiled and poor lawyers made. Though they have large powers of adjustment, individuals differ genetically in their tastes, powers and aptitudes. Respect for individuality is the great contribution of genetics to the treatment and understanding of human beings. To attribute everything to heredity, as some have done of late, is doubtless even more harmful than to attribute everything to environment; for it promotes a fatalistic viewpoint, it discourages effort. But to attribute everything to the environment is to encourage the disastrous belief that parent and teacher can fashion all their unhappy subjects on a uniform plan; is to promote that neglect of individuality which made education and home discipline in past generations one long cruelty. The human organism is a creature with extraordinary powers of adjustment to diverse conditions, with the capability of becoming many diverse things, of running through any one of many diverse careers. But the different individuals, in consequence of the fact that they are made of diverse combinations of materials, diverse genes, differ greatly in the way they respond to particular conditions; differ greatly in their capabilities of adjustment to the environment; differ greatly in their mentality, tastes, aptitudes; differ greatly in the work they will do and the careers they will follow, under a given constitution of society.

Relative Importance of Genetic Constitution and of Environment for Mental Diversities

What answer then can be given to the question so frequently asked: Which is more important, heredity or environment, for the mind and behavior of man? This question can be given a rational meaning, as remarked on an earlier page, only by converting it into a statistical question: Are more of the present differences in mentality and behavior the result of original diversities in genes, or of diversities in environment: diversities in education, social status, cultural state of the society in which men live, tradition, custom and the like?

No one can give numerical answers to this question. But certain general relations can be stated with probability. The answer to the question would be diverse, depending on the group of individuals concerning which the inquiry is made. For members of the same family, paradoxical as it may seem, the differences in mentality and temperament will probably be due more largely to diversity of gene combinations than to diversity of environment. The same is likely to be true for the differences between any small set of individuals belonging to the same social stratum, or living under similar cultural conditions; between the students at a given college, for example. Yet as we proceed to larger and more heterogeneous groups, the answer becomes less clear. In a single nation, as in the United States at the present time, there are certainly great numbers of diversities of both types; my own guess would be that the greater number of important differences are still those due to diversity of genes. As between nations of diverse cultures and traditions, the role of these environmental factors becomes greater, possibly equaling or exceeding that of genetic differences. As between groups of mankind at different epochs of history, it may be judged that the great differences are due to just what they appear to be—differences in knowledge, in tradition, in type of culture, in the accumulation of inventions, and the like; rather than to genetic differences in the populations at different eras.

Rules of Inheritance in Relation to the Mind

Since mental characteristics depend upon genes, they must, like other characteristics that depend on genes, be subject as generations pass to peculiarities of distribution, to rules of inheritance, that depend on the way the genes are distributed. Very great mental diversities, such as feeblemindedness in contrast to normality, manifest clearly these typical rules of inheritance; and the same is true for sensory diversities that are little affected by environmental conditions. But most mental characteristics are so greatly affected by the conditions under which the individuals live that rules of inheritance lose their sharp definition, become blurred and unrecognizable. Nevertheless, they continue to exist for the genetic constitution on which the diverse environmental conditions act. If it were possible to keep the conditions effectively uniform for a large number of individuals throughout a series of generations, the rules of inheritance consequent upon the known methods of distribution of the genes would clearly manifest themselves for mental characters. Under the diversified and changing environment of actuality their operation continues, and the results are still of great consequence for life and society; though what those results are must be deduced rather from general knowledge of the genetic constitution and its operation, than from sharply defined objective study of mental characteristics themselves.

The constitutional bases for mental diversities are bound to manifest the same types of phenomena described for inheritance in general in our first chapter. With every new individual there is put together a new combination of the genes affecting mental processes; a combination that may have never before existed. Half of the genes affecting the mind come from the father, half from the mother, and for every gene from one parent there is a corresponding gene from the other, the two forming a pair. The two genes of a pair from the two parents usually differ in their effects; sometimes sharply. In many cases one of them (the dominant gene) produces its characteristic effect, while the other (recessive gene) does not manifest itself at all in the mentality of the individual that develops from the combination. Defective or inferior genes are more commonly recessive; normal or superior ones dominant. Thus two mentally superior parents may each carry in a given pair one defective gene; some of their offspring will receive this defective gene from both parents, so that such offspring will be mentally defective, or inferior to both parents. Parents of high natural abilities may thus produce offspring that are dull and incompetent. Again, in the manner described in Chapter I, parents that are intellectually of low type may produce offspring that are mentally superior to themselves, through the contribution by the two parents of genes that supplement each other. That dependence of the characteristics of the offspring on the genes given to them by their parents, which we call heredity, may manifest itself in similarity of mentality and character between parents and offspring; or in marked dissimilarity in these matters. Intellectually superior parents may produce by recombination mediocre or inferior offspring; inferior parents may produce intellectually superior offspring. The appearance of geniuses—of Shakespeares, Keatses, Lincolns—in mediocre families is an example not of the failure of heredity, but of its method of operation.

Correlation in Mentality between Parents and Offspring

While all this is true, it is also true that with respect to mentality, temperament, character, the members of a particular family certainly have more genes in common that affect these matters than have individuals taken at random. The situation is in this respect exactly the same as for physical characteristics. Since this is the case, it must be expected that, other things being equal, members of a given family will be more alike in mentality, temperament and character than are persons taken at random, and this independently of the fact that members of the same family have similar environments. Sons will resemble their fathers in mentality on the average more than they resemble unrelated individuals, for they have more genes in common with their fathers. Brothers will resemble brothers, in temperament and character, on the average, more than they resemble persons outside the family. That is, heredity is bound to produce, on the average and in the long run, a certain increased degree of mental likeness between parent and offspring, between brothers, cousins and the like.

Studies made by Galton, Pearson, Terman and many others, show, as is well known, that in so far as mentality and temperament can be measured, individuals of the same family are indeed more alike in these matters than are individuals taken at random. A considerable degree of correlation between parents and offspring is found with respect to many manifestations of mentality and temperament.

But of course other conditions than genetic bases are never equal in such comparisons. The members of the same family have in considerable degree a common environment, differing from that in another family. One's family, with its instruction and training, and still more potent, its affections, attractions, repulsions, ideals, customs, traditions, is by far the most powerful complex of factors in one's environment. It can therefore be argued, as is done by Watson (who is in this supported to a certain degree by Pearl[4]), that the resemblances in mental characteristics between members of a family are due to these common features in their environment, rather than to their common genes. The common environment doubtless does indeed play a large role in these matters. But there is positive evidence, as we have seen, that diversity of genes affects mentality. This is bound to result, on the average, in a similarity of mental characteristics, as a result of community of genes, in closely related individuals. This may be obscured or nullified, in particular cases, by different environments and experiences, but in the long run is certain to manifest itself. Close relatives are, on the average, genetically as well as environmentally similar in temperament, mentality and personality.

Thus while mentally superior parents often through recombination of genes produce offspring that are mentally inferior, and mentally inferior parents often produce offspring that are mentally superior, nevertheless in the long run mentally superior parents must produce a greater proportion of mentally superior offspring than do inferior parents. In other words, a million superior parents will produce a greater number of superior offspring than will a million mediocre or inferior parents. But since the number of mediocre parents is many times as great as that of superior parents, it results that, absolutely considered, a larger number of the mentally superior individuals are produced by mediocre parents than by superior parents. Yet if the few mentally superior individuals produced no offspring, the proportion of superior individuals in the next generation would be to some extent, however small, reduced. The same is true for inferiority, and indeed for any particular type of temperament or mentality. Exclusion of parents of that type from reproduction would in some degree reduce the proportion of individuals of that type in the next generation, although the reduction might be very slight. So far as temperament and mentality depend on genes, this result is inevitable. These matters are taken up farther in our chapter on Eugenics (Chapter X).

NOTES AND REFERENCES ON CHAPTER VII

1. Page 160. See John B. Watson, *Behaviorism,* chapter V (New York, 1925).

2. Page 166. See H. J. Muller, *Mental Traits and Heredity: The Extent to which Mental Traits are Independent of Heredity, as Tested in a Case of Identical Twins Reared Apart.* Journal of Heredity, Vol. 16, 1925, pp. 433–449. Also H. H. Newman, *Mental Traits of Identical Twins Reared Apart.* Journal of Heredity, Vol. 20, 1929, pp. 49–64, 97–104 and 153–166.

3. Page 174. John Dewey, *Human Nature and Conduct; an Introduction to Social Psychology* (New York, 1922).

4. Page 184. See Raymond Pearl, *The Biology of Superiority.* American Mercury, Vol. 12, November, 1927. Also, by the same author, *Eugenics, Verhandlungen des V. internationalen Kongress für Vererbungswissenschaft,* Berlin, 1927, Bd. 1, pp. 261–282.

VIII

RECENT TRANSFORMATION OF THE KNOWLEDGE OF HEREDITY AND DEVELOPMENT; ITS BEARING ON INTERPRETATIONS OF THE INDIVIDUAL AND HIS CHARACTERISTICS

On the relations of heredity and environment to the characteristics and fate of human beings, sharply defined and positive assertions, often contradictory, have been set forth in the name of biological science. In one quarter —from the extreme eugenists—one hears that heredity is all, environment little or nothing. On that basis must be settled all the problems of humanity, with practical consequences that are startling. From the other side, Watsonian Behaviorism assures us that environment is all, heredity practically nothing, so far as concerns human affairs. And these contradictory doctrines beget a hundred others, incompatible one with another, but urged as the pronouncement of science. Mediation is attempted by division of the field: one set of characteristics is assigned to heredity; another to environment. But this gives rise to new disputes; many or most characters are claimed for each.

Trial and Error in the Progress of Science

The situation in a given field of science at a particular moment, the doctrines accepted or rejected, can be understood only by following the steps through which that situation was reached. Like other organic structures, the structure of science depends upon the way it has developed. Its present condition is greatly influenced by its recent experiences; at times in despite of sound reason and the state of the evidence. Discoveries that appear fundamental and that are incorporated into the body of science, sometimes turn out to be superficial or fallacious; discoveries that appear superficial and unimportant sometimes turn out to be fundamental. Readjustment to such changes requires time; and in the interval a discrepancy yawns between established truth and the formulations presented as science.

The state of scientific doctrine on the relations of heredity and environment illustrates these maxims. The growth and transformations of our knowledge of heredity and of its relations to environment are typical of the march of science. The advance of science is not a steady relentless progress over a wide front, making irretrievably its own the ground over which it passes; its methods and results impeccable, inerrant and infallible. Science is rather a human adventure, with all that this implies of ups and downs, of advancement and retreat, of success and failure. Science is mankind in the process of forming habits. Like other organisms, from the lowest up, mankind forms habits by the process of trial and error. The rat trying to find the way out of or into a maze is practicing the beginnings of science, and many of his operations are similar to those of human science. He is bound to follow up many false paths before he finds the right one, and at any given moment he may be headed up one of the false paths. It is necessary to follow the false one for a time, in order to discover that it is false. If we recognize that science does the same thing, that is not to condemn science, for that would be to condemn the process of learning.

But this method of progress leaves its marks on the body of science. Doctrines proven fallacious have a strange way of continuing an active and influential life long after their falsity has been shown. Illustrations of this fact abound in discussions of the biology of human individuals.

Notions of Heredity Reached in Early Stages of Knowledge

It is only in very recent years indeed, that there has been any systematic knowledge, such as may be called scientific, of the way in which the characteristics of descendants depend on what comes to them from their parents; only for the last 30 years. But in the pre-scientific period men's eyes and minds were busy with the matter, so that notions were formed about it; notions that still, unconsciously to us, play a great part in our conceptions of the subject. One of these notions, indefinite in character, was the conception of heredity as an entity, a thing in itself, set off from the rest of the universe; a force, as it were, tending to make the offspring like the parents, and opposed to another force or tendency, called variation or variability. This idea still underlies much discussion of the characteristics of individuals.

Unit Characters and Representative Particles

More precise and more obviously coloring all later knowledge were two ideas that gradually emerged as the pre-scientific period passed into that of scientific knowledge; two ideas that have had and still have enormous influence. These are the concepts of (1) unit characters, and (2) representative particles; particles in the germ cells representing the unit characters. Men saw that the children of two differing parents were not simply intermediate blends, but the characteristics of the two parents were separately transferred as units to the different children, where they formed a mosaic; so that the baby could be said to have his mother's fine eyes and the father's ugly nose. These were unit characters, therefore; things that are hereditary and that pass as units, from parent to offspring. This idea of unit characters became one of the corner-stones of the doctrine of heredity.

And from this idea of unit characters arose the second fundamental notion, that of representative particles. The unit characters are somehow transferred from parent to offspring by the way of the germ cells. There must then be something in the germ cell corresponding to each unit character, some minute particle. There must be a particle representing the shape of the nose, another the color of the eyes, another the color of the hair; another for acuteness of sight; others to represent musical ability, and so on. There must be a separate particle for each thing that can be transferred separately from parent to offspring. Such was the reasoning.

These two notions, of unit characters and of their representative particles, were destined to play an overmastering role in the attempts to understand heredity and its consequences. Though before Mendel men had not discovered the laws of transfer of the representative particles, in the passage of generations, the fact that they exist and are transferred seemed clear. Those who read of heredity in pre-Mendelian days will recall in the writings of Darwin, Weismann, Roux, and De Vries those theories of the regiments of particles which, under the names of pangens, ids, idants, and many others, moved in military formations through individuals into germ cells, and during development were distributed to the different parts of the embryo, causing each part to produce its characteristic structures.

Mendel's Discovery

The great discovery of Mendel, when it was recognized, seemed to confirm and give precision to these conceptions of unit characters and their representative particles. It enabled men to identify and delimit the diverse unit characters, and showed that they were distributed according to mathematical rules. When yellow peas were crossed with green peas, the green characteristic disappeared in the next generation; but reappeared again in the second generation, in the proportion of 1 green to 3 yellow. The green and the yellow were therefore unit characters; the one that disappeared in certain generations was called recessive, the other dominant. This proportion of 3 dominants to 1 recessive in the grandchildren was the most characteristic feature of what was called the Mendelian Law of the inheritance of unit characters. And further study by hundreds of investigators showed that great numbers of characteristics, in all sorts of organisms, including man, follow that same law.

To account for the Mendelian law, it seemed that the representative particles had to be brought in again. For where was the green, where is any recessive character, in the generation in which it does not appear? Since it does appear again in the next generation, it cannot have been really absent. It must have been merely hidden; there was still a particle representing it in the germ cells. The rules according to which the unit characters are transferred show us the rules of distribution of the representative particles in the germ cells; in no other way, it seemed, could the transfer of characters as units be accounted for.

Identification of the Representative Particles

And as time passed, the particles themselves were detected, seen under the microscope, given a local habitation and a name. As had before been suspected, it turned out that these representative particles are what make up the chromosomes within the cell nuclei. We now had visible things both for the unit characters, and for their representative particles or genes; the picture was complete. The history and methods of transference and distribution of the genes could be observed with the microscope; these corresponded point for point with the history, transference and distribution of the unit characters. In time it became possible, through the work of Morgan and his associates, to identify, as it were, the particles corresponding to particular unit characters; to discover in which one of the chromosomes they were situated, and in what part of that chromosome, with their precise position in relation to the genes representing other unit characters. The gene for white eye in Drosophila is near the left end of the first chromosome, at the distance 1.5 units from the end, and just to the right of the gene for yellow body color; in a similar way hundreds of genes were located. All this gave undreamed-of precision to heredity, and made possible advances in knowledge that a few years earlier had appeared inconceivable. All this was fundamentally correct, save for certain things in its interpretation.

As to the representative character of these particles there seemed no doubt: that is indeed what they were invented for, an invention confirmed by later discoveries. There was a particle, a gene, it was held, corresponding to, representing, and developing into, each of the later unit characters. In De Vries' paper announcing the rediscovery of Mendelism (1900) he remarked that "to every separate characteristic there corresponds a special form of material bearer," and that "the entire character of a plant is built out of definite units." This seemed indeed clear; it was commonly assumed, or explicitly set forth, in textbooks of genetics. This conception underlay all thought, all expositions of the matter; it is still potent.

What Characteristics Are Units?

A further task was to determine in detail what characteristics of organisms are thus units, and so are represented by these localized particles, these genes, in the germ cells. The test for this was at hand; any characteristics that follow the Mendelian rules, giving 3 to 1 ratios in the second generation, are behaving as units, are unit characters. Through years of investigation it was gradually worked out that unit characters include colors, dimensions, structures, both normal and abnormal, chemical peculiarities, physiological functions, sex, sensory, temperamental and mental characteristics. In final upshot it developed that all kinds of characteristics of organisms are of this sort; there are none that are not thus transferred from generation to generation as separable units of greater or less inclusiveness. *All* thus are represented in the chromosomes, in the genes. All characteristics are hereditary!

All Characteristics Hereditary

Magnificent and far-reaching discovery! We have learned then that all our characteristics, of every sort, come to us by heredity. Heredity determines in every respect what we are!

Every characteristic has its representative in the germ cell; by the unfolding of these the entire set that constitutes the organism is brought forth.

Such was the picture presented as the result of genetic research; all characteristics due to heredity—environment therefore, it was held, playing no part, or only the subordinate one of permitting or preventing the development of the organism, endowed at its beginning with its complete outfit of characteristics.

Bearing on Human Problems

The tremendous bearing of this on all biological problems, and particularly on human problems, was recognized and proclaimed; proclaimed in a chorus that grew louder and more voluminous as men came to realize its profound significance. On this fact of the all-might of heredity were to be based henceforth the conduct of life and the organization of society. "The New Decalogue of Science" proclaimed to the statesman that "heredity and not environment is the chief maker of men"; "that nearly all the misery and nearly all the happiness in the world are due *not* to environment; that the differences among men are due to differences in the germ cells with which they are born." It drew therefrom far-reaching practical conclusions; for example, "that the social classes which you seek to abolish by law are ordained by nature." Similarly radical doctrines met us everywhere. On this basis were to be settled the problems of education, the methods of dealing with criminals, the policy of the nation toward immigration; the regulation of the practice of curative and preventive medicine, of charitable organizations. In short, by this maxim were to be regulated birth and death, life and love, conduct and liberty. A logical corollary from all this was that the only cure for the ills of society lies in eugenics. Since everything is determined by heredity, our only hope for improvement lies in breeding a set of human beings with better hereditary qualities.

Further Discoveries

But while these doctrines were proclaimed, investigators continued to study in detail just what characteristics constitute the units and so are represented by single genes. And now puzzling paradoxical relations began to appear; things that clouded the crystal-clear concept of unit character represented by single genes; things that in the sequel become astonishing and revolutionary. The same characteristic in the same organism appeared in some experiments as a single unit; in others as a conjunction of many separable units. The eye in Drosophila was found to be a complex made from many distinct unit characters. Separate genes represent color, form, shape of facets, number of facets, and other structures and functions that make up the eye. The genes for these were identified and located; some were in the X-chromosome and gave sex-linked inheritance; some in the second chromosome, some in the third. Then came an experiment which showed that the entire eye, with all its parts and properties, is a single unit; eyes mated with eyelessness give single-unit Mendelian inheritance. The gene yielding the entire eye is in the fourth chromosome. What does this mean?

Same Characteristic Sometimes a Unit, Sometimes Many Units

In the same way the wing showed itself a complex made from a great number of separate units—colors, forms, structures, venation—each with its separate gene separately inherited; then the entire wing showed itself a single unit, tranferred as a whole. Hundreds of such cases presented themselves. The mind in man is a great complex, depending on many separate units; yet when normal mind is mated with feeble, each may behave as a single unit—normal mind as one unit, feeble mind as another.

How can the eye, the wing, the mind, be a single unit character, developed from a single representative gene; and be also a great complex of distinct unit characters, depending on many distinct genes? It began to be suspected that the notion of unit characters with single representative genes must conceal a fallacy.

Other experimental results led even more sharply to the same difficulty. We have seen that methods were discovered for locating precisely the particular genes on which characteristics depend; for showing in what chromosome, and in what part of that chromosome, each is placed. And now it was discovered that any particular unit character has genes all over the lot. Red eye color, mated with white, is a dominant sex-linked unit character with its gene at the point 1.5, near the left end of the X-chromosome. But when mated with pink, red is not sex-linked, but "typical Mendelian," a unit character with its gene not in X, but in the third chromosome, at the point 48. How can it have its representative in two different chromosomes? Again, it is mated with purple eye; red again behaves as a unit, now in neither X nor the third chromosome, but at about the middle of the second one. Or we mate red with vermilion; now its gene goes back to the X-chromosome, but is no longer near its end, at 1.5, as before, but is near its middle, at the point 33.

And this is but the beginning. By making other matings, the gene for red eye in Drosophila is found to be at dozens of different places in the chromosomes; the number thus far worked out stands at about 50. And this is typical; the same relations appear when other characteristics, dominant or recessive, are extensively studied in this or other organisms.

Single Characteristic Dependent on Many Genes

What does it all mean? Obviously, the idea of a single gene representing and developing into the single characteristic must go by the board. It is proved that red eye color depends upon 50 different genes, with others being added as time passes. It is demonstrated that 50 different parts of the germinal apparatus coöperate to produce this "unit character." The concept of red as a unit, depending on its single representative, is demolished. And this is a type; its history shows what is discovered when any characteristic is extensively studied.

But why then do they behave as units, passing as totals from one generation to another? It was, after all, their behavior as units that brought forth the concept of single representative genes. Have we here a contradiction in nature?

There is no contradiction. The answer to the question why they behave as units is simple, and once perceived, is illuminating. And with its perception, the entire theoretical structure formed of unit characters and representative particles, with the exclusive dependence of all characteristics on heredity, comes crashing to the ground—bringing with it all its consequences for life and society.

Why Characteristics Behave As Units

The situation is simply this: Any characteristic, as the eye with its color, is produced by the interaction of many different genes. These different genes have different locations in the chromosomes; and they have different functions, play different roles. There is one (or more than one) that is necessary if the foundation or beginning of the eye is to be laid down at all. If that one is defective, no eye is produced. Therefore, if one individual has this gene in the usual or "normal" conditions, that individual will produce well-developed eyes. If another has this gene defective (both members of the pair), it will have no eyes; such a race exists in the fruit-fly. If now, individuals of these two sorts be crossed, the descendants show Mendelian inheritance; that is, those that have either one or two of the normal genes have eyes, those with no normal gene of this pair have no eyes. Thus the entire eyes "behave as a unit character."

In other individuals this gene required for the foundation of the eyes is present in normal condition; but some other gene, required for producing the usual red eye color, is defective or modified; these, therefore, have eyes, but not of the usual red color. Crosses of these with individuals having red eyes again give "unit character inheritance."

Same Characteristic Inherited by Diverse Methods

Such is the situation with relation to any of the more than fifty genes whose coöperation is required for producing the normal eye. If two parents have all their genes normal and alike, except those of one pair, then we get "unit character inheritance" for just the difference made by this one pair of genes. In any such case this differing pair will have a precise location in the chromosome system, and the characteristics depending on it will be transferred in a particular way, depending on that location. If these genes lie in the X-chromosome the characteristics follow the sex-linked method of inheritance, if elsewhere, they do not. The two characteristics—say red eye and white eye—that depend respectively on the normal and the modified pair of genes, follow the distribution of the single differing pair of genes; and this is the secret of their acting as units.

If the difference between the two parents lies in some other single pair of genes that affect that character—genes located elsewhere—then the two characteristics follow the distribution of those two genes; the inheritance will now be of a different type. The parents may be so selected as to differ in respect to any one of the 50 or more genes that coöperate to produce red; in each case that characteristic follows the distribution of the genes that differ—showing what has been called unit character inheritance. Simple diagrams representing the genes and chromosomes, such as our figures in Chapters I and II, will show that this is bound to be so. "Unit character inheritance" means nothing but the kind of inheritance shown when the two parents differ in but a single pair of genes affecting the characteristic we are examining. But the parents may be so chosen as to differ in two pairs of genes, or three or more pairs that affect the characteristic; then we no longer find the latter showing unit character inheritance, but rather the so-called multiple factor inheritance. The same characteristic, in the same stock, gives in one set of matings typical Mendelian unit character inheritance, in another sex-linked unit character inheritance; in another set 2-factor inheritance; in another 3-factor inheritance; and so on, depending on the number and location of the genes in which the parents differ. This demonstration has been repeated for many different characteristics.

When, therefore, investigators continue to speak, as they do, of *"the gene"* for a characteristic, they must be understood to mean simply *"a gene"* for the characteristic; and specifically, that particular gene in which the parents differ, in the breeding work that they are carrying on. To say "the gene" for a particular character has no such absolute significance as was formerly given it; it is relative to the experiment that the speaker is thinking of.

Collapse of Unit Characters and Representative Particles

In sum, it turns out that what was called unit character inheritance does not indicate that the characteristic depends on but one gene. It tells nothing about the number of genes that coöperate to produce the characteristic. The conception of unit characters dependent on single representative particles is revealed as based upon a logical and material fallacy. Thorough work shows that every characteristic depends on the interaction of many genes, and that every gene affects many characteristics.

With the collapse of the concept of the unit character falls also the notion of the representative nature of the genes. The genes are units, in the sense that each kind of gene is a small localized body of material, which maintains with much tenacity its integrity, its peculiar constitution and properties, which reproduces itself, and which can be separated from the other genes that are present in the same cell, and can be combined with those from another cell. But no gene alone represents a characteristic or a structure of the organism; for every feature of the organism is a product of the interaction of many genes. The seeming unitary nature of characteristics is a reflection of the fact that the genes are units, and that often two parents differ in but one of these units, causing the characteristic to behave in inheritance as a unit. But the genes are the various diverse materials through whose interaction an individual is developed.

Resulting Change of Interpretation

All this shook to their foundations the conclusions that had been drawn from the study of inheritance, in its bearing on human affairs; particularly the conclusions as to the all-might of heredity and the unimportance of environment. It was not true, then, that each characteristic is passed on as such; passed on as a closed unit, complete in itself, and merely transferred from parent to offspring. On the contrary, the characteristic is built up by the interaction of many substances, many genes; if any of these substances are changed, the characteristic is altered. Is it certain then that other things, not genes, do not enter into this interaction? Is it certain that the environmental conditions have not a role here? May not alteration of the environment change the result, as does alteration of genes? Environmental influences are no longer closed off by the general theory of the matter. On the contrary, the situation is now seen to be such as to invite the participation of environmental conditions in production of the characteristics of organisms. It is no longer sufficient to determine merely whether particular characteristics depend on genes. It must further be determined whether they depend upon environment, and in what way. The whole subject is opened up anew for examination. Some of the results of that examination are summarized in our Chapters V and VI.

Transformation of Knowledge of Development

Thus far we have followed the students of heredity. A similar set of experiences was undergone by the students of development, investigators of the process by which the individual is derived from the egg. Corresponding to the notion of the representative nature of the genes, and supporting equally the idea that everything is determined by heredity, there prevailed what was called the mosaic theory of development. According to this, the genes representing diverse parts of the body were, during development, distributed to the different cells, some to one cell, some to others. What a cell became, what any part of the embryo became, depended upon what genes it received. The developing body was a mosaic of parts with diverse genes; this part of the embryo having the genes for the head, that part for the body; here for the eye, there for the ear or the heart, and so on. Each gene produced the part it represented.

There were many things in development that suggested the correctness of this view. The single cell with which the individual begins divides into two; one of these produces the right half of the body, the other the left. Is this because one contains the genes for the right half, the other the genes for the left half? In some animals when these first two cells are separated, each still produces only the half of the individual that it would have produced, if they had remained together. This agreed with the expectations of the mosaic theory.

Again, in a slightly later stage, such a creature as the frog has become a mass of small cells, and as we examine this mass, we can predict what part of the adult given cells will produce. All appears as if it were fixed and determined—as if by the distribution of diverse genes to different parts. In some of the later stages, if cells are removed from one region and transferred to another, they still continue to produce what they would have produced; an eye is thus developed in some part of the body where the presence of an eye is inappropriate and useless. All these and many other phenomena appeared to support the theory that the developing organism is a mosaic of parts bearing diverse genes, the latter producing diverse structures.

Disproof of the Mosaic Theory

But the growth of knowledge of development, like the growth of knowledge of inheritance, refused to move in unison with that conception. In our Chapters III and IV we have given an account of the situation in development that resulted in this appearance of agreement with the theory of a mosaic of genes. As shown in those chapters, what each cell becomes depends, not alone upon what genes it contains, but on its relation to other cells. It can be proved that the same individual cell will produce many different things, depending on what its cellular environment is. Each cell contains all the genes, and these genes interact with the cytoplasm, so modifying it as to produce the later tissues and structures. But the genes alter their interactions, depending on the surroundings of the cells that contain them, producing different structures under different conditions. After the genes have interacted with the cytoplasm so as to produce definite cytoplasmic parts, it may be impossible to change the fate of the cells; this is what gave rise to the deceptive appearance of agreement with the mosaic theory. But from the beginning development is adjustment of each cell to its cellular environment. For the details as to these relations, reference must be made to Chapters I, II and IV.

Nature of Development

On the whole, it turned out that the process of development is one of long-continued interaction of many chemicals, first supplied by the genes and the egg cytoplasm; producing great numbers of intermediate products, which by their further interaction produce additional substances, till by a series of stages the mature organism is reached. By the study of development, as well as by the study of inheritance, the genes are recognized to be a set of chemicals transferred to us from our parents, which by their interaction produce in a series of transformations the entire individual with all its characteristics and functions—no gene corresponding to or developing into any particular single characteristic. Different individuals start with different sets of these chemicals; they therefore develop different characteristics. A change in even a single one of these original chemicals may cause a great change in one or more of the features of the individual. But any gene merely enters into the general process of interaction, altering development and the products of development, in accordance with its peculiar nature.

Bearing on Interpretation of Heredity

Reflection shows that the theoretical and practical implications of this picture of the nature and action of the genes are fundamentally different from those drawn, consciously or unconsciously, from the conception of the single genes as representing, and developing into, the particular later characteristics. According to that notion, each individual enters the world with his outfit of characteristics complete; the account is closed at that point; everything that comes, comes by heredity. And on that fact are to be based our concepts and conduct of life, and our social practice. Many of the expositions of the relation of biology to social and other human problems have been based on that notion; some of them still are, to a small or great extent.

Relation of Genes and Environment in Development

When however we recognize that the genes are but chemicals, whose interaction with each other and with other things produces the organism—the adult characteristics being but the ultimate outcome of it all—then there is no *a priori* reason why those chemicals may not be added to, or subtracted from, or chemically altered; nor why their interaction should not be controlled by the conditions, so as to yield other characteristics. These possibilities are not closed off at the start, as by the other notion; they are opened up, as questions of fact, to be determined by experimentation. And experimentation has indeed shown that these possibilities represent realities, as we have attempted to show in detail in other chapters. The genes supply one set of materials and conditions for development, nutrition and environment another. How a given substance or condition affects development and its outcome depends, not on its source, not on whether it belongs to one set or the other, but upon its nature, and upon where and when it comes into action. To recognize these things displaces the entire subject from a basis of general principle and *a priori* argumentation to one of particular fact, of actual investigation of each case for itself. It takes down the sign of "no passing"; it opens the way for indefinite progress in the control of the development and characteristics of organisms.

IX

BIOLOGICAL FALLACIES AND HUMAN AFFAIRS

An eagerness to apply biological science to human affairs is a marked feature of the times. Gone are the days when the biologist was at best looked upon with amused tolerance; he is astonished to find himself called upon for advice, for leadership. He used to be pictured in the public prints as an absurd creature, his pockets bulging with snakes and newts—a harmless fellow, no doubt, but preposterous, objectionable. All that is changed. It has come to be recognized that man is a biological specimen, as much as are snakes and newts; his affairs are biological affairs, and must be carried on in accordance with sound biological principles. The uplifter hastens to secure the endorsement of the biologist for his particular remedy for human ills. The man in the street recognizes that if his practices are not biologically sound, they are not sound at all; the biological expert must set the seal of his approval upon them. Profound changes in practice are urged upon the world as pronouncements of biological science.

This seems the sudden and unexpected realization of a dream long cherished by the biologist. The world, then, is to be operated on scientific principles. The conduct of life and society are to be based, as they should be, on sound biological maxims! Books that lay down these biological maxims are among the best sellers. Biology has become popular!

But the enthusiasm of the biologist at this Utopian situation is dampened by doubts and worries as to the soundness of some of the maxims that are circulated in the name of biology. One begins to question if the science in its present state is adequate to the burden laid upon it. The situation is one that gives wide opportunities to the cocksure and uncritical, to those who are not troubled with doubts as to whether their science has solved the problems of humanity. There appear to be a lot of fallacies, or half fallacies, or quarter fallacies, circulating under the guise of biological principles applicable to human affairs, or underlying the practices that are proposed. Particularly abundant appear such fallacies in the attempts to apply to human problems, to social reforms, the results of scientific study of heredity. For some of these the biologist is not responsible; they are the work of middlemen, near-biologists—the popular writers that have undertaken to "sell" biology to the world. But others, it may be feared, are traceable to the biologists themselves.

It appears desirable to bring these fallacies forth into the light. And if some of them, contrary to the views of the present writer, are not fallacies but truths, bringing them into prominence will ultimately help to establish that fact.

Some of the fallacies lie in methods of thought; some are concrete scientific propositions; some are prescriptions for practice. Some are concealed, implicit—underlying conclusions, but never stated. Some are partial truths, in which the mixture of error is perhaps more potent than the infusion of truth. Many have their roots in the presentation of incomplete knowledge as if it were complete; in the persistence of mistaken conclusions after the discovery that they are mistakes; and in other all-too-human features of science.

In presenting them, attempts will be made to trace the fallacies to their sources in certain general methods of thought, and to partly classify them. In order to make them stand out, each fallacy will be given a brief formulation and a number; so that a sort of incomplete *Corpus Errorum Biologicorum* may result.

Perhaps the most general source of the fallacies lies in the fact that the human creature has two different ways of attacking questions that interest him; the rational and the empirical. On the one hand, based on experiences that have already come to him, he constructs concepts, categories, definitions, and by their use goes through an internal process called reasoning, from which he draws conclusions; on the basis of these conclusions he acts. His ability to reason becomes his pride; his faith in it becomes absolute; it is his distinction that he alone is a rational being. But on the other hand, he also observes and experiments; he thus acquires new experiences. In doing this, he carries with him his apparatus of concepts, definitions and categories, in which to store and classify what he thus gets. The questions he asks and the answers he expects depend on that apparatus. And he carries with him the conclusions that he has drawn, as a secure foundation on which to build farther; he carries with him his pride as a rational being.

But in experimentation, man comes into a direct and original relation with the universe. What comes to him by observation and experiment frequently ignores the questions he asks, ignores the concepts, definitions and categories carefully prepared for its reception, ignores or contradicts the conclusions that his reasoning has brought him. What is to be done? The common reaction is to jam things in as best one can, trim them down, throw out the parts that refuse to fit or that will not rest on the foundations prepared. This is often done unconsciously; one can't take in what one has no place for. Sometimes it is rationalized and justified. There is at present a concerted attempt to emphasize and defend the fact that what we find depends on the concepts and questions with which we approach natural phenomena. But exactly the distinctive work of science is the modification, the reconstruction, the abandonment of old ideas; the construction of new ones on the basis of observation. This however is a distressing operation, and many refuse to undergo it; even many whose work is the practice of scientific investigation. The old ideas persist along with the new observations; they form the basis—often unconsciously—for many of the conclusions that are drawn.

This is what has occurred in the study of heredity. A burden of concepts and definitions has come down from pre-experimental days; the pouring of the new wine of experimental knowledge into these has resulted in confusion. And this confusion is worse confounded by the strange and strong propensity of workers in heredity to flout and deny and despise the observations of the workers in environmental action; the equally strange and strong propensity of students of environmental effects to flout and deny and despise the work on inheritance. If one accepts the affirmative results of both sets, untroubled by their negations, untroubled by definitions that have come from the past, there results a simple, consistent and useful body of knowledge; though with less pretentious claims than are set forth by either single set.

Our first fallacy springs from the situation just described. It is:

I. The fallacy of non-experimental judgments, in matters of heredity and development.

This is a fallacy of general method, one of wide distribution, among professional biologists as among other men. It is the fallacy of judging, in these matters of genetics, on any other basis than close adherence to the detailed experimental results; the fallacy of judging propositions in genetics on the basis of one's general impressions of the rest of the universe; on the basis of what one sees in other fields. Heredity and evolution have so long been a subject for speculative exercises wherein one man's hypotheses were as good as another's, that almost everyone feels competent to put forth original notions on the matter. The time for that sort of thing is gone; there is now a great body of established observations which must form the basis for any judgments that are to be taken seriously. If ever there was a subject that shows itself unfitted for judgments of the *a priori* kind, of the inspired or happy thought type, that subject is genetics. Again and again have the wise pronouncements of the philosophically minded been upset, been flouted and jeered by the progress of experimental knowledge. Genetics and development are the domain of the unexpected. In those fields there has gradually shaped itself before our eyes a great system of relations and methods of action that has little resemblance to anything else that human beings have experienced; a system which, though it goes under the name of heredity, has little in common with the ideas that heredity brings to the minds of most persons, even at the present time; a system that to the biologically wise in their own conceit is foolishness; a system that can be properly grasped only by following most undeviatingly the observed and experimental results, with no concessions to general principles that are not merely statements of many observed facts in one proposition.

The opposition to this system, an opposition based on considerations drawn from other fields of work, though for a long period powerful enough to hold back its acceptance, has much crumbled of late, under the crushing weight of detailed and verifiable facts. But it still lurks, it still comes to light, though shamefacedly, and without the assurance that formerly characterized it. Gone are the days when to speak of chromosomes as matters of interest and importance was to give rise to ribald levity on the part of biologists that were not geneticists. But though the chromosomes themselves have become good form, it is still fashionable to reject with a superior air the detailed facts which give importance to the chromosomes. Young biological physicists with the confidence of youth and mechanism combined, still inform us that they "do not accept the gene," as if that did away with the immense mass of detailed evidence which requires the existence of those separable parts of the chromosomes, for which *gene* is the name. Such attitudes are still common. The extent to which investigators who in their own fields of work stick closely and loyally to the experimental facts, feel licensed to ignore and override those facts in other fields, is incredible. Whatever the situation in other fields, in genetics the opinion of a biologist who has not laboriously weighed the specific pertinent facts is of no value, however competent he may be in some other field.

And in this matter the proponents as well as the opponents of genetics must "watch their step." The relations brought forth in experimental genetics are so unexpected, so paradoxical, so difficult to fit into preconceived systems, that the temptation is strong to ignore those relations that are not what one's own favored system leads one to anticipate. This is particularly true when, as in genetics, the early results of experimentation fall into a simple system fitting a preconceived theory, as illustrated in the chapter preceding this. Under such conditions it is easy to lay aside as unimportant or unintelligible observations that do not agree with this theory. It is only by watching closely the details that disagree as well as those that do not, that a general doctrine adequate to reality can be formed.

Our second general fallacy is one that appears in the interpretation of observational and experimental results; it underlies most of the special fallacies seen in genetic biology. This is the fallacy that Morley in his life of Gladstone asserts to be the greatest affliction of politicians; it is indeed a common plague of humanity. It is:

II. The fallacy of attributing to one cause what is due to many causes.

This fallacy is the commonest error of science, making unsound a considerable proportion of its conclusions. Everywhere there is search for "the" cause of this or that phenomenon; the investigator is not content till he has found "it." Yet natural phenomena—and most emphatically is this true of biological phenomena—merely arise out of the complex situation in which they occur. Many elements of that situation affect them; and all that experimental science can do is to determine what difference is made by altering one or more of these elements; none is "the" cause to the exclusion of the others.

Investigators that recognize this have been heard to defend this fallacy as one necessary to inspire the worker; if he did not hope to find "the" cause he would not work. But it makes, too, the results of his work unsound, the conclusions drawn from them erroneous, the practices based upon them useless or pernicious. When he has found "the" cause, it follows that other proposed causes are not concerned in the matter, can be left out of account, must be rejected. From positive observations that one factor is at work, the conclusion is drawn that others are not; a vicious fallacy. This is our third general fallacy, an immediate child of the second:

III. The fallacy of concluding that because one factor plays a role, another does not; the fallacy of drawing negative conclusions from positive observations.

This fallacy contributes largely toward making science an entertaining spectacle; from it arise picturesque controversies. What the second investigator finds as "the" cause is not what the first one found; the subject is enlivened by a fight, which human beings love to watch. But if soundness rather than entertainment is the end, then it has to be recognized that any biological phenomenon arises through the interaction of many factors. It does not follow that because one cause has been found, others can be left out of account; yet that practice is astonishingly general. It is rather commonly safe to accept the positive assertions of an investigator, as to factors that are at work; one can almost as safely throw quietly overboard his negative conclusions, as to other factors that are not at work.

In biology the two last-stated fallacies appear in many guises. One of the commonest forms, and most prolific in error, is:

IV. The fallacy that the characteristics of organisms are divisible into two distinct classes; one due to heredity, the other to environment.

This notion is almost universal in the attempts to apply biology to human affairs. It is a form of the fallacy of single causes; a characteristic, it is held, must have as its cause either heredity or environment, as exclusive alternatives. This is a fundamental error, with vicious consequences. All characteristics are products of development, and development is always through an interaction of the "materials of inheritance," the genes, and other things, the environment. By changing genes characteristics are alterable; this is the observational ground for calling them hereditary. They are also alterable by changing the conditions under which the genes operate; this is the observational ground for calling them environmental. The same characteristic may be changed in either of these ways, as is demonstrated by many specific results of modern genetic investigation. The genes supply one set of conditions for development; their environment another; and the two sets need not differ in kind, nor indeed in effect. Most if not all characteristics are both hereditary and environmental, in the sense that both the genes and the environment take part in producing them, and that they may be altered by changing either.

The fallacy that characteristics fall into two mutually exclusive classes, one hereditary, the other environmental, was greatly favored in the history of genetics by the conception that hereditary characters are units complete in themselves, and each represented by a definite particle in the germ cell. This notion that each characteristic arose from a single unitary particle was itself the fine and ultimate flowering of the doctrine that things have but single causes. The later developments of biological science have demonstrated (as set forth in the preceding chapter) that the conception of unit characters developing from representative particles was itself a fallacy. Each characteristic arises through the coöperation of many genes, and through their interaction with other things, including environmental conditions.

The fallacy that hereditary and environmental characteristics are two distinct classes, along with other fallacies derived from it that are yet to be mentioned, has its roots partly in certain notions or definitions of what heredity is, that have come down to us from pre-scientific times. In their bearing and consequences these notions are fallacious; we shall therefore formulate them in our catalogue of fallacies, then discuss them. They are:

V. The fallacy that heredity is a force or entity, set off from the rest of the conditions of development, tending to produce resemblance between parents and descendants; the fallacy that heredity signifies something else than dependence of the characteristics of the individual on the materials (genes) that it receives from its parents, as manifested through change of characteristics when the genes are changed.

VI. The fallacy that heredity signifies or requires likeness, of parents and offspring; that it involves the maxim that "like produces like."

These notions were formed before there was sufficient basis for adequate conceptions or definitions; they are typical of many so formed, that now remain to haunt and confuse and mislead. Heredity was conceived as something that manifested itself in resemblance between parent and offspring. This resemblance was conceived as due to a force or entity, of unique character, a thing in itself. Sometimes "heredity" was thought of as the resemblance itself, sometimes as the force that produces this resemblance. In either case the phenomena that it designated were by concept and definition sharply separated from phenomena not due to this cause and not manifesting themselves as resemblance. This conceptual setting off of things that are hereditary from things that are environmental is still insisted on by some; to say that the same characteristic is both hereditary and environmental is to them the height of absurdity. The separateness in concept was there first; it has the right of priority, the right of way, whatever the observational facts.

Presentation of the notion that heredity means likeness as a fallacy brings two responses. One is to deny that it is a fallacy, to protest that that is indeed the meaning of heredity. The other is to assert that everyone knows it to be a fallacy; that no one holds that heredity requires likeness. What is certain is that to sum up heredity in the maxim that like produces like is most fallacious as an expression of the results of experimental genetics. The experimenter in genetics employs the term heredity as signifying dependence of the characteristics of the offspring on the materials received from the parents by way of the germ cells; a dependence which may manifest itself in likeness or in unlikeness between parent and offspring.

The idea of heredity as likeness between parents and offspring arose before the days of experimental genetics, and on the basis of observations that were valid. Comparing two different species of animals, like does produce like, in respect of their distinctive characteristics; this became the basis for the concept of heredity. Applying it to man, a confusing situation appears. Brown-eyed parents produce brown-eyed children; they also produce blue-eyed children. Is the former then heredity, the latter not? To the student of genetics both are equally heredity if either is; the same type of process underlies both. The color in both cases results from a peculiarity of the germ cells derived from the parents; it will be changed if the material of the germ cells is changed. This is what the student of genetics is discoursing of when he talks of heredity; not of likeness or unlikeness between parent and offspring. Dependence of the characteristics of the offspring on the materials derived from the parent may in many ways result in unlikeness between parent and offspring or between other close relatives. Two parents that are dominant with respect to given characteristics may produce offspring that are recessive for that same characteristic. Thus brown-eyed parents produce blue-eyed children; tall parents, short children; intelligent parents, stupid children; and these, with thousands of similar cases, are all examples of that dependence of characteristics on the genes that the geneticist calls heredity. Again, recessive parents frequently produce dominant offspring (when the recessive character is due to a different pair of genes in the two parents); in this way short parents may produce tall offspring, weak parents, strong offspring, stupid parents, intelligent offspring; and these too are examples of heredity. The operation of heredity, when statistically considered, results on the whole in a certain degree of likeness, of correlation, between the characteristics of parent and progeny, but this is a matter of averages, not of necessary individual similarities.

It was this notion of heredity as likeness and the cause of likeness that formerly made it appear impossible to discover any rules for heredity. It was this that gave origin to such pessimistic expressions as that set forth by a French author just before the revival of genetics:

"Heredity is a vain word. There are in it no laws to be drawn forth, and consequently no principles that can be stated.

There are simply certain curious remarks to be made—sometimes for, sometimes against, the transmission of virtues and vices by blood. And there are no more cases for than against."

It was only by abandoning this traditional idea of heredity as likeness that a systematic science of genetics became possible.

But in general discussions the traditional idea still reappears. The difference between the idea of heredity as likeness, and that implied by the experimental breeder, results in confusion, engenders a brood of fallacies. The student of man—the physician, sociologist, behaviorist—finds the biologist classing practically everything as hereditary (alterable through changing the germ cells). Interpreting this to mean that the offspring are like the parent in all these respects, and knowing of his own observations that this is not true in man, he may conclude that whatever the situation in animals, heredity has little role in man; genetics has no contribution to make to the understanding of human affairs. He rejects heredity and all its works, as applied to man. Or if he reads but to swallow, he may conclude that heredity is all, in man as in other organisms; that this means that like begets like, and that we are to proceed on that basis. He becomes a propagandist for eugenics as the only remedy for human ills.

All this may seem too crude for belief. No intelligent person in these days, it may be urged, can cherish the notion that heredity requires likeness; the cases in which it does not are too numerous and striking; are found in every textbook. The proposition has but to be stated, in order to be rejected. This is all true, yet the conception of heredity as necessarily implying likeness continues to play a great role in the attempts to apply genetics to man.

In these matters we have striking examples of a general fallacy of thought that plays a large role in science, as in other fields of human activity. It will be worth while parenthetically to formulate it and incorporate it in our catalogue. It is:

VII. The fallacy of basing conclusions on implied premises that when explicitly stated are rejected.

Many premises influencing reasoning are of this hidden, unconscious type. Such ghostly premises largely affect biological reasoning on the topics here dealt with; they underlie several of the fallacies already stated, and several to come.

The fallacies so far considered interbreed, producing offspring that loom large in discussions in human biology. Directly derivable from the fallacy that hereditary and environmental characteristics are two distinct classes, but resting also on a number of others, is:

VIII. The fallacy that showing a characteristic to be hereditary proves that it is not alterable by the environment.

This idea is widespread; one finds it set down as axiomatic even by investigators. Pearson sets forth that 50 to 75 per cent of the death rate of a certain population in man is determined fundamentally by factors of heredity, going on to the further conclusion that it is not capable of essential modification or amelioration by any sort of environmental action, and this conclusion has been widely quoted. The fallacy appears popularly in the notion of the inevitableness, the fatality, of what is hereditary; in the notion that if a disease or defect is hereditary "nothing can be done about it."

Yet there are now available a great number of characteristics that are inherited in typical Mendelian or sex-linked fashion, yet are readily modifiable or improvable by environmental changes. Such are, in the classic animal for genetic study, the fruit-fly, the conditions known as abnormal abdomen and reduplicated legs; such are the number of facets in the eye of this insect; such are the colors of maize plants; sex in various organisms; and many other inherited characteristics. No one that knows these cases can consciously accept the fallacy that because a condition is hereditary, it is not alterable by the environment.

The converse of this fallacy is likewise widely current:

IX. The fallacy that showing a characteristic to be altered by the environment proves that it is not hereditary.

This notion, as common as its converse, means when interpreted in the light of modern genetics, that if a characteristic is altered by changing the environment, it cannot be altered by changing genes; a preposterous error, as the results of experimentation clearly show. More in accord with our knowledge, but going somewhat beyond it, would be the assertion that any characteristic that can be affected by the environment can also be affected by a change of genes. It appears indeed probable, from the present state of knowledge and the trend of discovery, that the following sweeping statements will ultimately turn out to be justified:—

(1) All characteristics of organisms may be altered by changing the genes; provided we can learn how to change the proper genes.

(2) All characteristics may be altered by changing the environmental conditions under which the organism develops; provided that we learn what conditions to change and how to change them.

(3) Any kind of change of characteristics that can be induced by altering genes, can likewise be induced (if we know how) by altering conditions. (This statement is open to more doubt than the other two; but it is likely eventually to be found correct.)

The fallacy that showing a characteristic to be alterable through environmental conditions proves that it is not hereditary, is particularly common with medical men, sociologists, psychologists. The medical man resists the idea that heredity has a role in disease; because this appears to imply that nothing can be done about disease; that the conditions of life have no effect on it; and this he knows to be false. The social worker tends to reject any role of heredity in the affairs with which he deals, because this seems to him to imply that nothing can be done about social difficulties (save to breed a new race of men). It must be admitted that many biologists or near-biologists have helped to give them this impression; suffering themselves under the fallacy that heredity and environment are mutually exclusive in their action. The behaviorist rejects heredity in human behavior, because human behavior is readily modified by the environmental conditions; a consideration that in fact has no bearing on whether altering the genes alters behavior.

Among the farther fallacies produced by the interbreeding of those thus far considered, is one popular with certain propagandists of eugenics:

X. The fallacy that since all human characteristics are hereditary, heredity is all-important in human affairs, environment therefore unimportant.

This notion has been much pushed of late, by near-biologists, and to a certain extent by biologists; though happily a reaction from it is in progress. On this basis were to be settled the problems of education, immigration, public health, crime, charity—indeed all the problems of social organization. The growth of this dogma—based as it was on the now discarded notion of unit characters—has been sketched in the preceding chapter.

Those who fall into the fallacy of the all-might of heredity take one horn of a dilemma. Concluding that because experimentally things are hereditary they cannot be environmental, they disregard the equally experimental fact that they *are* environmental.

Another set takes the other horn of the dilemma. Looking only at the experimental fact that things *are* modifiable by environmental conditions, they fall into the converse fallacy:

XI. The fallacy that since all important human characteristics are environmental, therefore environment is all-important, heredity unimportant, in human affairs.

This notion is commonly held for the special field in which one has made personal observations; by medical men for disease; by sociologists for human society and institutions; by psychologists for behavior, for mental characteristics. All these things they find are affected by environmental conditions; hence it is concluded that heredity plays no role in them.

The most conspicuous recent example of this procedure is furnished by the Behaviorism of John B. Watson, which sets forth that in normal individuals inheritance plays no part in behavior, in abilities, in aptitudes, in character, in temperament, in what an individual becomes.[1] This is because Watson's studies reveal to him that these matters are deeply affected by environment, education, example, tradition, and the like. But it is only on the basis of a fallacious view of heredity that this yields the conclusion that heredity plays no role in them. To say that heredity does play a role is only to say that changing the genes with which an individual begins would alter the behavior, aptitudes, temperament or character of the individual; it does not in the least imply that education, example, tradition and the like have no effect; it says nothing about how great may be their effect. It is little short of a disaster that Watson should have tied up this doctrine of the powerlessness of heredity with his fine experimental results on the effects of environment, with his tremendously influential body of doctrine known as Behaviorism. A recent magazine author (Elmer Davis) has remarked that all up-to-date Americans are devotees of one of three Gospels: the Gospel of Mencken, the Gospel of Bruce Barton, the Gospel of Watson. And the Watsonian Gospel is the one that presents itself as the Gospel of Science. Just as it appears that biological science has succeeded in bringing to general recognition the importance of individuality, the fact that individuals differ greatly, in dependence on the materials of which they are made, Watson arrives with a super-biology to tell the world that this was all a mistake; and the world shows a tendency to swallow it! Nothing in Watson's positive observations requires such a negation. The whole appears to be a marked example of the fallacy of drawing negative conclusions from positive observations; of holding that the discovery of one cause requires the exclusion of another. To attribute everything to heredity is doubtless still more harmful than to attribute all to environment; but there is no need for either error.

From the more general fallacies thus far mentioned arise a number of practical fallacies or partial fallacies; fallacies that underlie discussion and proposed action, though they may not be formally expressed. Some of these are quantitative rather than qualitative, leading to the expectation of great consequences where slight ones are indicated. Based largely on the fallacy that heredity signifies likeness is:

XII. The fallacy that preventing the breeding of hereditary defectives will largely or entirely get rid of such defectives in later generations.

Though every student of genetics knows this to be a crude fallacy, we meet it everywhere in popular discussion. Feeblemindedness, insanity, deformity, tuberculosis, crime—these things are hereditary. Therefore in the next generation such as exist will have arisen from the correspondingly defective parents of the present generation, for like produces like. Therefore, cut out the defective parents and you will not have the defective offspring. Such is the reasoning.

Any society that succeeds in carrying out this plan is of course in for a great disappointment. The great majority of the defective genes causing such troubles are present in normal individuals. These are bound to produce a considerable proportion of defectiveness in the next generation. Stopping the propagation of the actually defective individuals of the present generation does get rid of a number of defective genes, and in the case of serious defects, this should by all means be done. But to encourage the expectation that this will solve the problem of hereditary defects, close up the asylums for feebleminded and insane, do away with prisons, is only to subject society to deception.

The corresponding fallacy with respect to superior individuals is equally common:

XIII. The fallacy that superior individuals must have come from superior parents; and that this will continue to happen.

This notion has so strong a hold that when superior men appear whose ostensible parents have given no evidence of superiority (as happens in a very large number of the cases), it is concluded that there must be some mystery as to the parentage; that we must be mistaken as to who the parents are. Or we must labor to prove that the parents were in fact superior individuals, though they gave no sign of it. We must find superior parents for Lincoln, for Keats, for Shakespeare, although history provides none, because "like produces like." Even investigators in human heredity are at times so under the domination of this idea that they deliberately hunt for cases to confirm it, and ignore those that do not confirm it, poisoning the stream of knowledge at its source. In printed contributions to the subject, cases of distinguished individuals that have distinguished relatives are emphasized as significant; the more numerous cases of those that have not are passed over as of no significance.

Experimental biology does not support this notion. From parents of two very inferior varieties of corn come offspring that are superior to both. From two parents with hereditarily defective eyes, in the fruit-flies, come offspring with perfect eyes. From two parents that are weak and short-lived come offspring that are vigorous and long-lived. The coming together of complementary genes from the two parents, producing in the offspring something not found in either parent; and the converse separation in the offspring of the parents' complementary genes, so as to give different characteristics—these play a very great role in inheritance. If we are to speak of the inheritance of characteristics (as is commonly but inaccurately done), then we are forced to say that the child may inherit vigor and long life from parents hereditarily weak and short-lived; ill health and short life from parents that are vigorous and long-lived; foolishness from wise parents; great ability from parents that are ne'er-do-wells. Superiority and inferiority depend in very large measure on the way the genes coming from the two parents happen to be combined; and any pair of parents can produce thousands of diverse combinations. Examination shows that in man a very large proportion of the individuals recognized as superior come from parents that give no evidence of superiority. The few children coming from the small class of superior parents do indeed show a larger proportion of superior individuals than those from mediocre or inferior parents. But owing to the fact that the latter classes contain many more individuals, the absolute number of superior offspring produced by them is much greater than the number produced by the superior parents (see Chapter VII).

At times there emerges the crude notion that if the intellectually superior persons of one generation stop breeding, the next generation will be without such. The difference so made would beyond question be extremely slight; though if this were continued for many generations the cumulative result might become perceptible or considerable.

From the two fallacies last considered arises further:—

XIV. The fallacy that biology requires an aristocratic constitution of society.

The notion that biology supports the theory of democracy, in the sense that all individuals are fundamentally alike, is a recognized fallacy—though Watson, at the head of the Behaviorist cohorts, is endeavoring to rehabilitate it. From this recognition it is concluded in certain quarters, by one of the commonest types of fallacious reasoning, that since biology does not support democracy, it must support the theory of aristocracy. The "New Decalogue of Science" informed us that "the classes that you wish to get rid of are ordained of nature" and much more to that effect.[2] We meet popular articles calling biology to witness that the only sound or possible constitution of human society is an aristocracy.

This conclusion is based on the notion that like produces like; that intellectuals produce intellectuals; genius produces genius; morons produce morons; good people produce good people; criminals produce criminals; that each grade of ability, of superiority or inferiority, reproduces itself. As already emphasized, the study of genetics does not support such a view. If we may attempt to summarize what genetics indicates as to the constitution of a human population, we find something like this:

In any fairly large sample of a human population, whatever its average status, whatever the uniformity resulting from the way it is selected, there is reason to expect that in the next generation marked inequalities will appear, physical, temperamental, intellectual, moral. There will be a few that are much superior to the rest; a few markedly inferior; and in the great intermediate mass a strong differentiation in tastes and aptitudes. The human species, reproducing biparentally, is constituted like the bodies of many organisms that have a high power of regeneration. From any limited portion, even if relatively uniform, there can be reproduced all the different parts, adapted to different functions; can be reproduced the entire social organism, with all its differentiations. The "classes" do not perpetuate themselves as such. From the higher many lower are produced; from the lower, many higher. From the great mediocre group are produced more of the higher than the higher group itself produces; and more of the lower than the lower group itself produces.

This is far from being an aristocratic constitution of society, in the sense of a continuity and self-perpetuation of classes. It is equally far, no doubt, from being a democracy, in the sense that all individuals are alike. But if one means by a democracy such a constitution of society that any part of the mass can in time supply individuals fitted for all its functions—in that sense the biological situation is that of democracy. It is the kind of democracy that President Lowell called for in his book on Public Opinion and Popular Government—a democracy that produces experts; perhaps not an unsatisfactory constitution of society.

Positive Contributions of Genetics to Human Affairs

The enumeration of these fallacies may leave the impression that the biological study of heredity and environment has had little but fallacies to contribute to the management of life. It is true that its positive contributions to human life have been less immediately practical than those coming from biology in the fields of medicine, hygiene and public health. The successful application of biology to social and racial problems is a most difficult matter. Genetics, the biological science dealing with these subjects, is but young; its age is 30 years. What it has already brought to light has, when rightly and conservatively estimated, important bearings on the problems of society. Its most important contribution is that which Behaviorism denies: the truth that human beings are endowed with diverse tastes, temperaments, aptitudes, diverse ways of responding to the same conditions. And that therefore, as Davenport[3] has well put it, there can be no adequate *impersonal* science or art of medicine, of hygiene, of education; of any matter that deals with human beings. Always the nature of the particular individual dealt with must be taken into consideration.

What promises to be a second major contribution of this branch of biology lies in the recognition that certain individuals carry genes so defective that they should not propagate; a matter to be dealt with in the next chapter.

And there is even now coming into view the discovery of how genes become defective, of how the hereditary constitution is injured, a matter taken up in chapter XV. A beginning has been made, and when that lead is fully worked out, it promises one of the greatest contributions to the biology of man and to the practice of human life.

NOTES AND REFERENCES ON CHAPTER IX

1. Page 217. See John B. Watson, *Behaviorism* (New York, 1925), Chapter V; also by the same author, *The Behaviorist Looks at Instincts,* Harper's Magazine, Vol. 155, 1927, pp. 228–235.

2. Page 220. A. E. Wiggam, *The New Decalogue of Science,* The Century Magazine, March, 1922.

3. Page 222. C. B. Davenport, *Heredity in Relation to Eugenics* (New York, 1911), Preface.

X

WHAT CAN WE HOPE FROM EUGENICS?

DOMESTICATED animals and plants have been greatly improved by selective breeding. Why should not the same thing be done for man? This project of improving the human stock through selective breeding is called Eugenics.

What are the prospects for such improvement? What may we hope from eugenics? To some the promise of eugenics appears very great. "We must endeavor to show," says the President of the American Eugenics Society, "that eugenics supplies the most effective and permanent solution to the problems that have been so ineffectually dealt with hitherto by physicians, public health officers, social workers, clergymen and reformers—the problems of combating disease, disability, defectiveness, degeneracy, delinquency, vice and crime."[1] And Bulletin No. 26–10 of that Society, discussing "crime, pauperism, unemployability, etc.," asserts in its foreword that "As soon as eugenics is properly comprehended, the solution of the problems above mentioned will naturally follow."[2]

The conviction underlying these great hopes is something as follows: The troubles of the world, and the remedy for these troubles, lie fundamentally in the diverse hereditary constitutions of human beings. Some men are strong, healthy, wise, virtuous. Others are weak, foolish, diseased, immoral, criminal; and it is these that cause the troubles of the world. Laws, customs, education, material surroundings, are the creations of men and reflect their fundamental nature. To attempt to correct these things is merely to treat superficial symptoms. To go to the root of the troubles a better breed of men must be produced; one that shall not contain the inferior types. When a better breed has taken over the business of the world, laws, customs, education, material conditions will take care of themselves. Good men, wise men, will make a good world.

This is to be brought about through the fact that the qualities of men have a hereditary basis, a basis in the genes; their characteristics are "hereditary." The thing to do is to see that succeeding generations are produced by individuals with desirable characteristics; produced by the healthy, the strong, the wise, the virtuous. Then later generations will consist of individuals that inherit these desirable characteristics; they will be healthy, strong, wise, virtuous, and the troubles of society will be largely at an end.

This seems a magnificent vision; it has aroused the enthusiasm of many men. "The first commandment that biology gives to statesmanship," said "The New Decalogue of Science," "is the duty of eugenics." [3] Societies have been formed to propagate this plan. "Eugenics," says the President of the American Eugenics Society, "is incomparably the greatest concern of mankind." [1]

How far are such hopes justified? What results can be expected from eugenic procedures? For what problems of society is the effective solution through eugenics in present sight? What is the biological status of the proposal to improve the human race by selective breeding? What are the methods that must be used? And how practicable are these methods? What sort of an enterprise is it on which we are embarking in the project of eugenics? Is it a long-range undertaking, whose time scale is centuries or millennia? Or is it something that will presently give tangible results? Is it simply an attempt to give to slow evolutionary processes an upward rather than a downward trend, in the belief that a thousand years hence the world will be better for it? Or is eugenics a present remedy for present ills? Or is it a mixture of these things?

Further, what is the relation of eugenics to other measures proposed for improving the lot of mankind? What is its relation to plans for improvements in education, in health, in social organization, and in other environmental conditions? Does it render these unnecessary? Is it indeed antagonistic to them, as some have held, demanding their abandonment, as causing racial deterioration?

For insight into these matters, one must have in mind the biological situation; must consider carefully how differences among individuals are brought about through diversities in the materials that they receive from their parents. We must keep before us a picture of the working of heredity. If we fail to do this, we are certain to delude ourselves. Some of the details of the workings of heredity are the fundamental, the decisive, points in answering the question: What can we hope from eugenics?

These details have been presented in Chapters I and II, so that they will not be repeated here. And it must be emphasized that the present chapter will be unintelligible if one has not in mind the main outlines given in Chapter I.

The Problem of Eugenics

The problem of eugenics is presented by the existence and action of defective genes, inefficient genes, inferior genes. Seriously defective genes result in the production of individuals that are imperfect: feebleminded individuals, persons that early become insane, deaf, blind; persons whose blood refuses to coagulate; persons that are weak and short-lived, or that are extremely susceptible to tuberculosis or other infections. Genes that are relatively inefficient produce individuals that are dull, inconstant, lacking in self-control, lacking in initiative; and so on through the long list of undesirable qualities that are found in man. More efficient genes produce the individuals that we call superior. As set forth in Chapter I, the number of grades, the number of types, of diversity in characteristics produced by differences among the genes is practically infinite. And the diverse types of genes are combined in an infinity of different ways, in different individuals, giving rise to the very great differences in native endowment observed among human beings. Many of the differences so produced are not fittingly characterized as matters of superiority or inferiority, but rather as diversities in tastes, mentality, aptitudes and character; those diversities which supply workers for the different tasks of the world, and which make of humanity a varied pageant. But others are clearly matters of defectiveness, or of decrease of efficiency; such are feeblemindedness, insanity, blindness and the like; such are stupidity, and in general all decreased power of adjustment to the conditions.

Eugenics desires to prevent the occurrence of individuals manifesting the effects of defective genes, inferior genes, and to replace these with individuals having better gene combinations.

Is the Aim of Eugenics a Desirable One?

Leaving aside for the moment the question of practicability, is this aim a desirable one? With relation to the more extreme defects, such as insanity, or feeblemindedness, this question will hardly be raised. Individuals with these defects are without value to themselves or to the rest of the world. Their replacement by normal individuals would be advantageous from every point of view.

But the question has been raised with respect to lesser defects and weaknesses, even though in themselves undesirable. For such defects may coexist with high qualities in other respects. Serious physical defects may be accompanied by high intellectual powers. Robert Louis Stevenson, William De Morgan, Chopin, were tuberculous. Would it have been better if these men had been replaced by others? Prevention of the production of all gene combinations bearing even seriously defective genes would beyond question result in the loss of certain men of great value to the world. Should the aim of eugenics therefore be relinquished?

The value of the eugenic aim can be estimated only from its total results, taken in the long run, as compared with the total results of some other line of action. Its ultimate aim is not the mere suppression of certain types of individuals, but their replacement by other types. The replacement of individuals that lack resistance, that are weak, inefficient, susceptible to illnesses, by persons that are strong, efficient and healthful; the replacement of the stupid, unstable and foolish by the quick, constant, intelligent—this would obviously bring about certain results that are highly desirable. Is there reason to suppose that it would result in the production of a smaller proportion of persons with high intellectual or artistic qualities; fewer Stevensons, De Morgans, Chopins?

Certainly there is no ground for supposing that it would result in fewer genetic combinations capable of such intellectual or artistic attainments. It has sometimes been contended that physical defects act in many cases as intellectual stimuli, through the principle of compensating action, or otherwise, thus resulting in great achievements that would otherwise not have been accomplished. Such action may play a role in some cases, but its importance will not commonly be adjudged very great; certainly not so great as to outweigh the benefits of replacing defective individuals by normal ones. Injuries, sorrows, and misfortunes will never be so completely driven from the world, by eugenics or other means, that humanity cannot gather from them such stimuli as they afford. No biological achievement could be greater than to provide that all individuals born shall be free from serious genetic defects.

"Tampering with the Germ Plasm"

Against all action in the direction of eugenics is at times raised the meaningless cry that men must not "tamper with the germ plasm." To tamper with the germ plasm can mean only to so act that the germ plasm in the future will be different from what it would be if one acted otherwise. But no normal human being can avoid this. Every individual is custodian of a portion of the germ plasm; he cannot avoid determining its fate, and thereby altering the germ plasm combinations of the future. Every individual that begets children or that refrains from begetting children tampers with the germ plasm; it will in the future be different in consequence of his conduct. Every individual that chooses one mate rather than another tampers with the germ plasm. The priest that does not marry tampers with the germ plasm; it will be diverse as a result of his conduct. Every person that limits in any way the production of offspring, or that does not limit it, tampers with the germ plasm. The proposals of eugenics are merely that attempts shall be made to employ common sense in the unavoidable effects of conduct on the germ plasm of the future, so that this germ plasm shall be better rather than worse.

Is the Aim of Eugenics a Practicable One?

But can this end be accomplished? Is the aim of eugenics a practicable one? A number of different measures are available, or have been proposed, for preventing or remedying the effects of defective genes or for, in the long run, replacing defective individuals by normal ones. These measures may be classified into three categories: First, therapeutic or other environmental measures may be taken. Second, by proper matings, inferior genes may be so combined with superior ones that the defective genes have no effect, or little. The methods by which this is brought about constitute what may be called family eugenics. Third, attempts may be made to get rid of defective or inferior genes, to exclude them from the race. This may be called racial eugenics. All of these three methods may have a certain effectiveness, but the ultimate or long-range consequences are very different for the three.

Therapeutic or Environmental Measures

The genes do not act independently of the environment. On the contrary the individual is produced by the interaction of genes and environmental conditions; so that the same set of genes may yield diverse characteristics under diverse environments. This has been set forth in preceding chapters.

Under certain conditions, therefore, a given set of genes may produce a defective individual; under other conditions, a normal one. The defectiveness of the individuals could therefore be prevented either by starting them with a different set of genes, or by changing the environment in which they develop. In the fruit-fly, as we saw in Chapter V, defectiveness of a certain gene produces under ordinary conditions an abnormal structure of the abdomen. But if the individuals are kept in a dry atmosphere, the abnormality does not appear. A change of environment has prevented the effects of a defective gene. Other examples of such action have been given in the same chapter.

Similarly, in man, certain combinations of genes yield an individual that is unusually susceptible to infection with tuberculosis. But if infection is prevented, or if the resistance of the individual is increased by proper living conditions or by therapeutic measures, he does not succumb to tuberculosis. Such prevention, by environmental means, of the consequences of weak or imperfect genes plays a very great role in all matters of susceptibility and resistance. Essentially the same in general principle is the effect of education, training and the like, in changing the behavior that would without it result from the genes present in the individual. In some of these matters the effects of genes and environment are inextricably intermingled. Behavior is bound to be relative to environment, it cannot be dealt with as dependent on genes alone. A given set of genes may result under one environment in criminality; under another in the career of a useful citizen.

At times genes are so defective as to fail to produce materials required for the proper development or functioning of the organism; hormones may be produced that are deficient in quality or quantity or both, and this results in serious later defects. If the thyroid secretion is defective, the individual fails to develop normally; it becomes a cretin, an idiot. If insulin is not properly formed, diabetes results. If the sex hormones are not normal, intersexuality or some other discordant condition follows. Many similar results may follow from the operation of defective genes.

Chemical therapeutics has discovered of late that such disorders due to defective genes can be remedied. The consequences of a defective thyroid secretion are remedied by introducing the thyroid hormone with the food; the pitiful cretin becomes a normal human being. Lack of insulin is similarly remedied by introduction of insulin from outside. The necessary chemicals can even be synthesized, made artificially, as recent revolutionary researches show. In principle it is clear that defects in the store of chemicals given us in heredity may be supplied by other means; although as yet this has been accomplished for relatively few of the serious defects resulting from imperfect genes.

Remedying the effects of defective or inefficient genes by environmental measures has been decried, as preserving and perpetuating the inferior genes, and so as leading to the deterioration of the race. How far this objection is justified we shall consider in another chapter. But the fact that environmental agents affect only the product of the genes, not the genes themselves, is of the very greatest consequence. It is only the single individual treated that is helped by therapeutic or environmental measures. Although he himself becomes normal, his genes remain defective to the same extent as before. These defective genes multiply in his body and are transmitted to his descendants; so that the latter too must be subjected to treatment if they are not to be defective. The cretin that has become normal through the use of thyroxin transmits his defective genes unchanged to his children: they too must be treated with thyroxin. And this is typical; the defective genes are not themselves improved through environmental action. The use of remedial measures must be repeated in every generation. Therapeutic and other environmental measures therefore provide no thorough-going permanent remedy for defectiveness of genes.

Family Eugenics

The measure most employed throughout organisms for preventing the effects of defectiveness of genes is to give the defective gene a normal companion gene, that shall perform fully the required function. This is accomplished, as set forth in Chapter I, by giving organisms two parents, each of which supplies an exemplar of every kind of gene required, so that the individual has not merely one gene of each kind, but two. He thus has two chances instead of one of getting each function in development properly performed. If one gene of a pair is poor, the other is likely to be better, and it is the latter that usually produces its effect. The poor gene therefore does no harm; it is masked, protected by the better one. If the poor gene is the one that makes imperfect blood, which fails to coagulate, this is remedied by the presence of the normal gene, and the blood is normal. If the poor gene tends to yield an inefficient brain, a stupid individual, even to the extent of feeblemindedness, the presence of the other gene makes the individual normal. This method of action prevails for a very great number of characteristics.

This method goes far in preventing injury from defective genes, although it depends to a considerable extent on chance. If two defective genes come together in the same pair, an imperfect individual is produced. But in the long run the method is effective. It is practiced on a large scale by almost all organisms. Man has taken hold of it, carried it farther, incorporated the plan into customs and laws; practices it systematically in what we shall call family eugenics. Family eugenics is a system of rules for insuring that the children of a particular mating, a particular family, shall not be defective; for insuring normal families. What these rules try to do is to provide that there shall be at least one high-class gene in every pair; they try to provide that any defective gene shall be protected by a normal one that accompanies it. In brief, they try to prevent two defective genes from getting together in the same pair. The two main maxims of family eugenics as commonly set forth, are about as follows:

1. Persons belonging to families, any of whose members show instances of similar defects, should not mate, even though the two persons are themselves normal. For each may bear, in the hidden or recessive condition, one of the defective genes to which the personal imperfection is due. And since each parent contributes to the offspring one gene to each pair, these two hidden genes may get together in the same pair, whereupon the child produced will be personally defective. This method of action was illustrated in figure 7 of Chapter I.

2. The second maxim of family eugenics is that close relatives should not mate. Close relatives are persons who have gotten a considerable proportion of their genes from the same ancestors. If some of these genes were defective, as is very probable, in view of the commonness of defective genes, then the two relatives will have certain defective genes in common. Their mating may then bring together two defective genes into the same pair, resulting again in imperfect offspring. The danger of this of course decreases as the degree of relationship decreases. In families known to bear important defects, all mating between even distant relatives should be avoided. In families without indication of serious gene defects the mating of cousins, for example, is not likely to result in the production of imperfect offspring.

These two rules of family eugenics are of course rendered more effective by the preservation of careful records of family history and relationship. In some organisms there are effective physiological methods of preventing the mating of close relatives.

The two maxims of family eugenics are special cases under the general rule that so far as possible the two parents should contribute to the children genes that supplement each other, the father supplying good genes for the pairs that are poor in the mother, the mother supplying good genes for the pairs that are poor in the father. In this way offspring may be produced that are superior to either parent; that have none of the defects of either father or mother. Some details of the way this works out have been given in Chapter I.

It is obvious that the methods of family eugenics, like the therapeutic and environmental methods of preventing the effects of poor genes, do not get rid of the defective or inferior genes. The defective genes are by these methods merely hidden. They are indeed by the methods of family eugenics protected, allowed to multiply, and passed on to descendants. As generations pass, they are bound to come to light again, producing individuals that are defective or inferior. The longer the defective genes have been kept concealed and inactive, the more certain it is that their presence will be unknown, so that individuals bearing the same defective genes in recessive condition may mate. Thereupon some of the offspring receive two defective genes in the same pair, and are therefore personally defective. As has before been set forth, a large proportion of the defective or inferior individuals that exist in a human population are thus due to recombination; to the getting together of two defective genes that have been kept apart by the methods of family eugenics. They arise from parents that are themselves normal, but that bear hidden defective genes.

Thus family eugenics is by no means a permanent or radical remedy for defective genes. The defective genes continue to exist, in concealment; they are carried about in normal individuals and there multiplied; they are passed on to descendants. In time they come to light, producing defective individuals.

Racial Eugenics

By the methods of family eugenics, as we have just seen, defective genes are conserved, perpetuated, multiplied; and in time their effects appear. Really to stop the appearance of defective individuals, to get them out of the race, as the eugenist wishes to do, we have to get rid of the defective genes, not merely to cover them up, as is done by family eugenics. The proposal to get rid of defective genes, instead of merely hiding them, we may call racial eugenics. It is this that is mainly in the minds of those that propose eugenics as a remedy for the ills of humanity.

The problem for racial eugenics then is: How shall we get rid of the defective genes, poor genes, so that their effects shall not appear again? The practices of family eugenics not only do not help in this, but are the great obstacle to racial eugenics. They hide the defective genes and cause them to be distributed everywhere. What can be done actually to get rid of the defective genes?

There is only one way of getting rid of defective genes, so that they shall not reappear. And that way is simply that the individuals bearing the defective genes must not produce offspring. In no other way can the career of defective genes be stopped. This then is the fundamental method of racial eugenics.

But who are the individuals that bear the defective genes? For any particular defective gene that is recessive, such as that for feeblemindedness, for hæmophilia, or the like, there are, as we have seen, two classes of bearers. On the one hand there is a relatively small number of persons that bear two of the defective genes in a pair, so that these persons are themselves defective. They are the feebleminded individuals, the heritably insane, the deformed, the weak, the degenerate. These individuals are of course recognizable, and their propagation can be stopped; this is the measure proposed by eugenics.

But in addition to these there is a much larger number that have but one defective gene in the pair, the other member of the pair being a normal gene. In these persons the defective gene has no effect, although in later generations the effects will appear. They are like the carriers of the typhoid bacillus that are themselves immune to the disease. Though themselves unaffected, they hand on the source of ill to others. There is no direct way of identifying these carriers of defective genes. Some of them may be known from family histories, but in the great majority of cases neither the individual himself nor anyone else is aware that he is a carrier of a defective gene. Consequently it is not possible to stop their propagation, so that there is no direct means of removing from the race the defective genes borne by them. These hidden defective genes borne by normal individuals are much more numerous than the manifested ones borne by individuals that are themselves defective. In the case of feeblemindedness it has been calculated (as will be set forth later) that there are about thirty times as many normal individuals having the defective gene as there are feebleminded individuals.

How Are We to Get Rid of Defective Genes?

These hidden defective genes are the greatest obstacle to the program of racial eugenics. In view of their presence in great numbers, the problem of eugenics recurs with great emphasis: How are we to get rid of defective genes?

This, it is sometimes urged, is merely a problem of technique; it is a question for practical breeders. Look what has been done for the breeds of cattle and poultry; look what has been done for cultivated plants! Must not the same methods applied to man give similar results? Shall we use our knowledge of genetic science for the improvement of cattle and fruit, while the infinitely more important improvement of the human stock is neglected? There exist human beings that are vigorous, wise, virtuous. Human characteristics are heritable. Why then should we not, by the known principles and practice of scientific breeding, produce a population composed of the vigorous, wise and virtuous, thus solving at once the problems that have been so ineffectually dealt with by other methods? It is up to the professional geneticists to give us the method for this.

Method Used in Improvement of Animals

The method can in fact be readily given. There is no obstacle in the known principles of genetic science to the production of such a result, provided we can decide what qualities we wish to conserve in our human stock, and provided that the necessary methods are applied with the necessary thoroughness for the necessary length of time. The difficulties are not in the rules of inheritance; not in the theory of breeding, but in its practice. They lie essentially in the conflict between observance of the rules of family eugenics, whose effect is to keep defective genes hidden, and the requirements of racial eugenics, which demands the uncovering of the defective genes, that they may be eliminated. We have in man a set of organisms that have been for ages, and still are, devoting themselves to covering up, protecting, hiding, their defective genes, and thus allowing them to be multiplied. What is required is that they cease to do this; that they mate in such a way as to bring the defective genes to light; and that the individuals which then show their effects must be restrained from propagation. To bring this about, to improve the human stock as cattle have been improved, a practical breeder must be placed in complete control, with instructions to fear not God neither regard man, in the execution of his project. He need have little acquaintance with the subtleties of genetic science. His method of work is simple, but in its application his motto must be "Thorough." He will mate a few individuals possessing characteristics as near the desired ones as he can find, and he will stop the propagation of the rest. Then he will proceed to bring to light the defective genes, by reversing the rules of family eugenics. The selected progeny of his first cross will be inbred, as cattle are inbred. This will bring together on the one hand defective genes, on the other, desirable genes; the results will appear in the personal characteristics of the individuals produced. A great stock of defective and deformed individuals will appear, along with a number that are not defective or are less defective. Those showing undesirable traits will be again eliminated; the rest again inbred. By a continuation of this process, with at times judicious crossing of superior individuals, followed by farther inbreeding and elimination, the defective and undesirable genes will gradually be uncovered and removed from the race. In this way, after many generations, after many centuries, a race will have been produced, all of whose individuals show the combination of characteristics sought; a combination of the highest characteristics found in man (so far as none of these are incompatible with the others). The obstacles to the production of this result lie, it must be repeated, not in the theory of the matter, but in its practice.

But obviously, the practical obstacles are insuperable. This plan will not be carried out. Humanity will not deliberately set itself to producing defective offspring, in order that the genes which are responsible for the defects may be brought to light, and so eliminated by stopping the propagation of those that bear them. Humanity will not give up family eugenics. Humanity will not confine reproduction to a few individuals selected as superior by a practical breeder. Lay that proposition before any of the democratic peoples of the world, and see what the answer will be.

This procedure then is not within the bounds of practicality. The methods applied to domestic animals cannot be applied to man. The comparison of the two cases is misleading, is not a guide to what can be done or what results can be expected in man.

What Eugenic Measures are Practicable in Man?

The question of racial eugenics for man becomes, therefore: What eugenic measures are practicable, considering that man is the sort of creature he is? What methods can be employed, while retaining the practices of family eugenics, that hide the defective genes? And what result can be looked for from these?

It is of course possible to identify the individuals that bear two of the defective genes to a pair. These are the individuals that are themselves defective. Further, in the infrequent cases of dominant defects, even the individuals that have but one defective gene are personally defective; such is Bar-eye in

Drosophila; such is brachydactyly (short fingers) in man. In all these cases, we have a chance to put an end to the careers of at least certain examples of the defective genes. The measure practically proposed by eugenics is to stop the propagation of the defective individuals; to stop the propagation, for example, of the feebleminded individuals; to stop the propagation of all individuals showing the effects of seriously defective genes.

Cessation of Propagation of Defectives

This is certainly a desirable measure. In the case of genes so defective as to cause feeblemindedness, it is difficult to see how anyone could raise a doubt as to this. It is incredible that anyone should knowingly advocate continuing the operations of defective genes that produce such frightful results as idiocy or insanity. To stop the propagation of the feebleminded, by thoroughly effective measures, is a procedure for the welfare of future generations that should be supported by all enlightened persons. Even though it may get rid of but a small proportion of the defective genes, every case saved is a gain, is worth while in itself.

To what classes of defective or delinquent or inferior individuals is this measure applicable? To how many of the ills of the world is there a complete or partial remedy in stopping the propagation of the individuals suffering from them?

This measure can be applied to all serious ills that are due to defects in a single pair of genes. In such cases, the difference between the defective individuals and those not defective is sharply defined. In the case of ills that result from a combination of several defective genes in diverse pairs, there are many gradations or degrees, in different individuals, so that the cases which should be stopped from propagation are difficult to define. The known number of single-pair gene defects that are so serious as to make it practicable to stop the propagation of the affected individuals, is as yet small. Feeblemindedness is doubtless the clearest case, although not all instances of this are due to gene defects. Hæmophilia, the defect of blood that results in bleeding to death from any wound, is a clearly marked case of a single-gene defect. Some cases of insanity probably belong in this group, though seemingly many do not. Probably there are cases of goitre, of diabetes, of epilepsy, of susceptibility to tuberculosis, of susceptibility to cancer, that are of this type. It is true that in most of these cases there is uncertainty as to how large a proportion are due primarily to gene defects and how far environmental conditions play a role. There is very great need for more knowledge as to what troubles of humanity are fundamentally due to single-pair gene defects. Investigations in this field are difficult, but essential, if the program of eugenics is to be made even moderately effective. So fast as serious single-pair gene defects are identified, those affected with the troubles that they produce must be brought to cease propagation.

It must be recognized however that there are great difficulties. All degrees of defectiveness occur, grading into normality. In many types of defect, the environmental conditions have much to do in deciding whether the trouble shall appear, and in what degree. These things make the decision difficult as to whether stoppage of propagation is required. Compulsory measures, laws, can probably be applied to but few of the defects; mainly to those which bring the affected individuals into public institutions. More can be done by educating social workers and medical men to take this matter seriously, that they may give warning, by spreading abroad a knowledge of these matters; and by arousing the conscience through an understanding of the consequences of propagation by persons bearing such defects. But to make this work effective, increase of knowledge on these matters is greatly needed. With such increase of knowledge, the list of defects to which this measure can be applied may in time become large.

How Far Does This Get Rid of Defective Genes?

To stop the propagation of persons bearing serious hereditary defects is most worth while. But in considering eugenics as a remedy for social ills, the further question must be raised: How far does this stoppage of the propagation of the defective individuals go in correcting the evil? How far does it go in getting rid of the defective genes, so that their effects will not reappear in later generations? To what extent does it reduce the number of defective individuals in the next and later generations? How far will this go in solving the problems of "combating disease, disability, defectiveness, vice and crime"? To what extent and how soon will it close asylums and prisons?

In the relatively small group of dominant defects, stopping the propagation of all the defective individuals would clear the defect from the race in a single generation. In such cases, every individual bearing even one defective gene is himself defective, so that if all such cease propagation, the defective gene at once disappears. If all defects were of this type, this eugenic measure would be an effective and immediate remedy for them.

But in the much larger group of recessive defects, stopping the propagation of the defective individuals affects only one of the two classes of individuals that have the defective gene. It leaves untouched the great class of normal "carriers," the individuals bearing but one defective gene in a pair, protected by a normal companion gene. Can an estimate be formed of the relative numbers of individuals in the two classes, and as to the result of stopping the propagation of but one of them?

Feeblemindedness as an Example

Such an estimate can be made. To illustrate the situation, feeblemindedness may be taken as a type. It is the simplest and least affected by the environment of any of the defects with which eugenic measures can deal. How effectively can they deal with feeblemindedness?

Statistics indicated some years ago that the feebleminded made up about one-third of one per cent of the population; so that in a population of a hundred million there were about

330,000. So far as these are cases of heritable feeblemindedness, they are the individuals that have in a single pair two of the defective genes that produce feeblemindedness. From this proportion, it is possible to compute, by known relations, approximately the proportion of normal individuals that bear one of the defective genes. It turns out to be about 10 per cent of the population. If the number of feebleminded is 330,000, the number of normal carriers of the gene is about ten millions. For every individual bearing two of the defective genes, there are about 30 normal individuals bearing one such gene.

Thus the population of the country consists of three groups: there is the small group of about 330,000 feebleminded, carrying two defective genes to the pair; there is the group of about 10,000,000 normal carriers with one defective gene to the pair; and finally there is a group of about 90,000,000 normals having none of the defective genes of this type.

The feebleminded of the next generation come on the one hand from the small group of the feebleminded; on the other, from the large carrier group. In addition, new carriers are formed by mating of individuals from these two groups with individuals from the normal group. By stopping the propagation of the feebleminded group, the production of feebleminded individuals and of carriers from that group is ended. But their production from the carrier group is not affected. What proportion of the feebleminded are thus gotten rid of for the next generation?

The answer to this question depends to a certain extent on how widely scattered in the population are the defective genes. If they are widely scattered, the calculations of R. A. Fisher[4] indicate that about 11 per cent of the feebleminded of any generation come from the mating of feebleminded of the previous generation, while 89 per cent of them come from matings among the carrier group. Thus by stopping the propagation of the feebleminded of the present generation, we get rid of about 11 per cent of the feebleminded of the next generation. That generation still contains 89 per cent produced by the carriers. If the original number of feebleminded was 330,000, in the next generation the number is about 293,700.

This procedure has affected very little the reservoir of carriers, so that it remains nearly what it was. In a third generation it still produces about 290,000 feebleminded—even though the feebleminded themselves are not allowed to propagate. That is, by entirely excluding the feebleminded from propagation, in present and future generations, the number of feebleminded is reduced at the first generation by about 11 per cent; thereafter very little progress is made in reducing their number.

As generations pass however, there is a slight further reduction, resulting from a small decrease in the number of normal carriers. This is due to the fact that none of the feebleminded will now mate with normals to produce additional carriers. But the decrease due to this cause is slight. It has been computed that if the proportion of feebleminded in the population is one per thousand, to decrease that proportion to one per ten thousand will require about 68 generations, or two to three thousand years, if it is done merely by stopping the propagation of all feebleminded individuals. In the main, the eleven per cent reduction at the first generation is what is accomplished by this measure.

If the defective genes are not widely scattered through the population, then a greater immediate effect would be produced by stopping the propagation of the feebleminded individuals. Fisher estimates that possibly a reduction of 30 to 40 per cent might in such a case be produced.

A reduction in the number of feebleminded by eleven per cent, or still more, a reduction by thirty or forty per cent, would be a very great achievement. And it could be brought about in no other way than by stopping propagation of the feebleminded persons.

A parallel result can be expected when this same measure is applied to other sharply defined single-pair gene defects. It is probable that in most cases the defective genes are not gathered in special groups of the population, but scattered at random, so that reduction of the number of defective individuals will be slow. Further, the smaller the proportion of defective individuals among the normals, the slower is the reduction in number that results from stopping the propagation of the defective individuals. But it is clear that when individuals bearing such defects are allowed to propagate, the number of defectives is increased; when their propagation is stopped, the number is decreased. Even though the reduction may not be very great, the pertinent maxim is: Every case prevented is a gain.

Yet this measure of eugenics, though having a certain effectiveness, is obviously far from solving the problem presented by gene defects; even by gene defects so sharply defined as to make practicable the entire stoppage of the propagation of the afflicted individuals. The majority of those affected—in most cases probably the very great majority—arise in each generation from the class of normal "carriers." And these carriers are little affected by the measure proposed.

Dependency and Delinquency

Further, most of the difficulties of society come from individuals that do not show single sharply defined pathological traits, such as insanity or feeblemindedness. Rather are they individuals and families of low economic status, requiring the attentions of charity organizations; or delinquents that disturb the social order and are subject to the ministrations of the law. The conditions to be met are those of poverty, pauperism, idleness, "unemployability," delinquency, and criminality, in its many gradations. What are the prospects for dealing by eugenic measures with these matters? What are the prospects of getting rid of the dependent, delinquent, and criminal classes?

What is the biological status of such individuals? In all or most of such cases we are dealing with behavior, with reactions to the environment; reactions which are inefficient or harmful. All such reactions depend both on the genes—the constitution with which the individual starts—and on the nature of the environment. By altering either, the reactions would be changed. A great complex of interdependent causes it at work.

Environmental conditions certainly play a large role here. Certain psychologists attribute most or all of the undesirable traits of character shown by individuals to shocks and injurious influences operating during early childhood. It appears beyond doubt that these play an important part. Along with these, frequently go poverty, with consequent loss of opportunity; defective or harmful education; bad traditions; bad social organization; specific misfortunes. Estimates of the weight of these and other environmental matters differ greatly. Here no simple biological principle is decisive; it is as clear biologically that environment affects behavior as that constitution does; and biology furnishes no automatic method of determining the relative role of each. Only familiarity with the conditions actually found in dependent or delinquent individuals or families, resting on a basis of acquaintance with genetics and with the other springs of behavior, can yield a valuable judgment.

But in such groups it cannot be doubted that on the whole less favorable gene combinations accompany the unfavorable environmental conditions. That is, in the dependent or delinquent group, the gene combinations contain on the average a larger number of genes that must be classed as at least relatively defective, and these are present in many cases as "double doses"—as two unfavorable genes to a pair. Such groups form a reservoir of less favorable genes, as compared with the reservoir of more favorable genes in the self-supporting group.

This difference must not be exaggerated. The same sets of genes found in the dependent groups would in other combinations result in individuals that were self-supporting, efficient, or even superior; this through the contribution by the parents of complementary genes, in the way described in earlier chapters. This often happens in the production of offspring within such groups. In the same way, from parents of superior types, new combinations of genes may result in offspring that are so inferior as to become under certain conditions dependent or criminal. There is by no means a sharp separation or an impassable barrier between the two sets of individuals; for by recombinations within each group, individuals fitting the other group are produced. But on the average, a greater proportion of poor genes will be found in the delinquent group, a greater proportion of better genes in the self-controlled, or self-supporting group.

It is obvious that in this situation both environmental and eugenic measures, effectively applied, might yield results. In single cases, as in large groups, substitution of better genes for poor ones would improve the situation, even though the outward environment were unchanged. Or supplying more favorable conditions would improve the situation, even though the gene combinations remained the same. What may be hoped from the one compared with the other depends on the comparative practicability of the two sets of measures, and on the time required for them to be effective.

The application of eugenic measures in such a situation is extremely difficult. In these matters we are dealing not with simple, single-pair gene defects, but with bad combinations of genes, taken in conjunction with bad environmental conditions. By changes in the gene combinations, successive generations pass from one group to the other. It is hard to imagine a more elusive task than the prevention of the formation of those combinations of genes that under certain conditions produce stupid, delinquent or criminal individuals. If all such persons were prevented from propagation, other conditions remaining the same, this would make only a very little difference to the number present in the next generation. It may be doubted whether the change would be detected except by refined statistical examination. If the only remedy for criminality is to "cut it out of the germ plasm," as has been asserted, then indeed we shall have the crime wave with us for a long time.

But there is no basis in the science of biology for the assertion that this is the only remedy.

Certainly therefore every other remedy that has possibilities should be tried while we are waiting for eugenics to do its perfect work. And it is probable that changes in environment —changes in treatment of infancy, in education, in tradition, in customs, in ideals, in economic situation and the organization of society—can do much more for the ills of society than can be done through direct attempts to change the genetic constitution of the population. With respect to criminality, this opinion has recently been set forth by Davenport,[5] himself a strong advocate of eugenics. If punishment could be made prompt and certain, so that individuals would not be tempted to take a chance, this would probably do more in a few years for the suppression of criminality than can be expected in a very long period from eugenics. As compared with what we can hope from eugenics, for all the dependent and delinquent classes, save in extreme cases of single-gene defects little affected by the environment, much more is to be expected from changes in conditions of life; certainly much more in the short period of a century or two. We must cling to anything that these environmental changes can do, for what they accomplish they can do promptly, in a generation or two; while changes in these matters by means of eugenics will require immensely long periods.

Yet eugenic measures have their scope also; they may operate slowly, in the same direction as environmental improvement. While the dependent and delinquent classes are not sharply separated from the rest of society, they carry on the whole a larger proportion of poor genes than do the rest. This being so, certain measures can be and have been suggested that would slowly decrease the proportion of poor genes in the population, and in so far improve the breed of mankind. It is proposed in general that by appropriate measures the propagation of the dependent and delinquent groups shall be lessened, that of "superior" groups, the more efficient or intelligent individuals, be increased. Methods suggested for doing this are: that habitual criminals be not allowed to propagate; that the present ban on the dissemination of knowledge as to how to decrease the number of offspring produced be removed, so that such knowledge may become available to the less efficient or intelligent groups; that the economic status of individuals of superior intelligence or abilities be in some way raised; that the conscience of both groups be aroused, so that the more intelligent and efficient shall deliberately produce more offspring, the less intelligent and efficient fewer.

All these measures would probably have some slow statistical effect in shifting the constitution of the population in the direction of the classes whose propagation is increased and away from those whose propagation is decreased. This effect *must* follow if the genetic constitution is, in the mass, correlated with the characteristics of the population, as it certainly is.

Slowness of Eugenic Action

There have been exaggerated hopes as to the rapid effectiveness of these and similar proposals, based mainly on the deceptive maxim that "like produces like." This maxim is correct for organisms that multiply by buds, cuttings and the like; in general it is true for all cases in which offspring are produced from a single parent only, as happens in many plants and lower animals. In such reproduction, new combinations of genes are not made, so that the offspring have the same genetic constitution as the parents. "A Baldwin apple produces only a Baldwin apple," but in human beings the situation is very different. With relation to human characteristics on which depend "superiority" and "inferiority," the maxim that like produces like is largely fallacious. The "inferior" individuals possess largely the same genes as the "superior" ones, but in less fortunate combinations. One individual may possess all that brings a man into the superior class, except ambition or industry or patience. Or his genes may predispose him to disdain of worldly distinction; or to scattering his efforts in many objects of interest. Mated with another undistinguished individual, who bears, hidden or manifest, genes that supply the missing qualities, certain of the offspring may receive a combination that includes all that is required for distinction. In characteristics taken singly, an individual so produced may not be superior to his undistinguished parents, or to most members of the stock to which he belongs; but his qualities supplement and support one another, placing him in the front rank. And when he reproduces, the combination that gave him superiority is taken apart; his offspring may relapse again into the normal obscurity. From the great mass of mediocre parents arise more superior offspring than from the few distinguished parents; more inferior offspring than from the inferior parents. And superior parents often produce mediocre or inferior offspring; inferior parents at times produce mediocre or superior offspring. In consequence of this situation, decrease or even complete stoppage of the propagation of the "superior" individuals, or of the "inferior" individuals has very little effect on the average grade of the next generation.

Although all this be true, nevertheless in the long run an effect is produced. A million "superior" individuals doubtless produce a somewhat greater proportion of "superior" offspring than do a million inferior individuals. This will be true whatever one's definition of the terms "superior" and "inferior," or whatever characterizations are employed in place of them. Since genes affect characteristics, any large group showing a specified type of characteristics has more genes tending to produce that type of characteristic than has another group. Therefore, by increasing the propagation of the "superior" groups and decreasing that of the "inferior" groups, the general level is, however slowly, raised. Changes brought about in this way will be enormously slow, measurable in thousands of years rather than in short periods. Yet the general effect is to divert the trend of evolution from downward to upward, so that in a thousand years or more humanity may be the better for them. They may therefore claim the support of persons who desire that this shall be accomplished.

Two Great Advances Required

For more effective action than is now possible for improving the race through eugenic measures, and particularly for getting rid of marked single-gene defects, two great advances in knowledge and in practice are required.

Recognition of Normal Carriers of Defective Genes

One of these is an advance in knowledge which, if it could be brought about, would tremendously increase the effectiveness of eugenic measures. What is required is some method of recognizing the carriers of defective genes: persons that are themselves normal, but have one defective gene in one of their pairs.[6] To discover methods of identifying such individuals would be one of the greatest biological discoveries that could be made; one of the most fruitful in immediate practical application.

For such extreme defects as result in feeblemindedness, this seems not outside the range of possible future discovery. In many cases, in animals and plants, the bearers of a single defective or recessive gene that has a normal or dominant companion, do differ in certain respects, usually little marked, from individuals that have both genes normal. It seems not impossible that by refined chemical tests or by other tests, individuals bearing but one of the genes that induce feeblemindedness might be identified. When that is done, if ever, such normal "carriers" of the feebleminded gene could be brought to cease propagation. If that were thoroughly done, eugenic measures could totally remove hereditary feeblemindedness from the race in a single generation; could close institutions devoted to that class of dependents. And the same could be done for other ills due to any serious gene defects of which the normal carriers could be identified. There is no prospect that such a discovery could be made once for all, for every sort of defective gene. Detailed studies would be required for each type; special methods devised for each. Investigations extending for many years will be demanded before such discoveries can be widely extended. To promote such investigations in human genetics is probably now the most direct way to further the welfare of future generations through eugenic measures.

Need for Improved Environment, for Eugenic Purposes

The second advance in knowledge and practice is almost equally necessary, and will become still more indispensable if that first advance is made. We must know more as to what human troubles are due to definite single-pair gene defects. These are the defects with which eugenic measures can effectively deal; and as yet but a small number of them are positively known. The great difficulty about this is that bad living conditions often produce the same kind of results that bad genes do. Persons may become idle and worthless, insane or criminal or tuberculous—either through bad genes or bad living conditions, or through a combination of both. So long as living conditions are bad, we do not know what ills are due to poor genes. We must therefore correct the bad living conditions, not only for their directly beneficial effect, but also for the sake of eugenics. When this is done, it will be possible to discover what defects are primarily the result of defective genes, and then to plan measures for getting rid of these genes: measures for stopping the propagation of their carriers. That is, as a preliminary to the effective work of eugenics other reforms must be carried through. Measures of public health must be carried out, overwork and bad conditions of living done away with, faults of diet, both quantitative and qualitative, corrected; economic ills conquered, grinding poverty abolished. When these things are done, when the human plant is given conditions under which it can unfold its capabilities without stunting, poisoning and mutilation by the environment, then it will be possible to discover what ills are due primarily to defective genes, and to plan such measures as are possible for their eradication. Acting on such precise knowledge, far more rapid and effective results may be hoped for than from the present blind action in merely encouraging the propagation of certain classes, discouraging that of others.

Prospects for Eugenics in the Future

When thus particular troubles can be positively attributed to particular gene defects, and when, if ever, it becomes possible to detect the normal carriers of the defective genes, then humanity will have in its hands the power completely to suppress such troubles within a generation. Feeblemindedness can be brought rapidly to disappearance, and with it hereditary insanity, inherited tendency to tuberculosis or cancer, in general, hereditary weaknesses, abnormalities and degeneracy, in so far as these are the result of single-pair gene defects. To join with energy in present attempts to correct the environmental evils of society is one of the two most important steps for the advance of eugenics. Until the preventable environmental ills are largely corrected what eugenics can do is relatively little. The other important step toward increased efficacy of eugenic measures is to promote the advance of genetic science, that the normal carriers of defective genes may become identifiable.

Even with our present knowledge, eugenics may enable us to get rid of a certain proportion of such defectives as the feebleminded. Beyond this it represents, in the present situation, an aspiration, a hope, rather than a present remedy for present ills. It is an attempt to place ourselves in line with upward evolution, and as such is worthy of interest and active sympathy; but it must not take the place of efforts for improvement of the conditions of life. Whether eugenics is to become something more quickly practical than this depends upon whether certain requisite discoveries are made by the science of genetics.

NOTES AND REFERENCES ON CHAPTER X

1. Pages 223 and 224. *Report of the President of the American Eugenics Society,* Professor Irving Fisher, June 26, 1926. Published by the American Eugenics Society.

2. Page 223. Leon F. Whitney, *The Source of Crime.* Christian Work Magazine (with a foreword by the Editors). Reprinted as Bulletin No. 26–10 of the American Eugenics Society.

3. Page 224. A. E. Wiggam, *The New Decalogue of Science.* The Century Magazine, March, 1922.

4. Page 241. R. A. Fisher, *Elimination of Mental Defect.* The Journal of Heredity, Vol. 18, 1927, pp. 529–531. See also E. M. East, *Hidden Feeblemindedness.* Journal of Heredity, Vol 8, 1917, pp. 215–217, and R. C. Punnett, *Eliminating Feeblemindedness.* Journal of Heredity, Vol. 8, 1917, pp. 464–465.

5. Page 246. C. B. Davenport, *Crime, Heredity and Environment.* Journal of Heredity, Vol. 19, 1928, pp. 307–313.

6. Page 249. The great importance of discovering methods of recognizing individuals who, though themselves normal, carry seriously defective genes, is emphasized by E. M. East, in the paper referred to in Note 4 above.

XI

THE BIOLOGICAL BASIS OF MARRIAGE AND THE FAMILY

THE present is an era for questioning of all human institutions. Marriage and the family do not escape. Are they breaking down? Can they be so modified as to fulfil better the needs of human beings? Can some substitute be found for them? These are matters at the present time much discussed.[1] It is worth while in such a discussion to examine the biological origin of these institutions, and the biological needs that they fulfil. No substitute can succeed that does not answer these needs.

Marriage and the Family Not an Invention of Man

Marriage and the family, even life-long monogamous marriage, are not an invention that is original with man. These institutions, in various forms, have been worked out independently by many different organisms.[2] There is little doubt that our ancestors had them before they were men. Certainly many organisms that are not men now have them.

The various manifestations of marriage and the family have their basis in the interplay of the great underlying physiological processes of organisms; in the interrelations of development, metabolism, behavior, reproduction. These fundamental activities are divisible into two sets that are to a certain extent in opposition, sometimes in extreme opposition. On the one hand organisms live individually; on the other hand they reproduce. Each individual has its own life career; it grows, develops, seeks and takes nutrition, pursues its varied business and desires, becomes mature; most finally becomes old and dies. And in addition each produces new individuals that shall take his place when his individual career is closed.

Interference of Reproduction with the Individual Career

Now all organisms find—as human beings find and some loudly proclaim—that the business of reproduction interferes with their careers. The two things interact, intertwine, modify each other. This occurs differently in different organisms; there result many diverse systems, diverse institutions. Among these diverse systems are the family, in its various types and gradations, as we find it in man and in other animals. The number and variety of systems arising from the interaction of reproduction with the pursuit of the life career are so great as to defy enumeration. But an examination of certain typical situations will illustrate the role of the family.

Different Systems

The life career of some organisms is so simple, and their reproduction is so simple, that there is little interference. In some of those favorites of the amateur microscopists, the rotifers, the individual simply drops here and there pieces of itself, which grow into new individuals. There is no mating and there is no further relation of parent with the offspring. Yet even here the life career is somewhat modified; part of the parent's nutrition goes into these pieces, and their separation from the parent may be a severe operation.

Single-Parent System

And even in such cases the beginning of the family may appear. In some animals the piece or germ remains attached to the parent body, there growing and developing, feeding through the parent's mouth and sharing the parent's career. Several such offspring may remain attached to one parent; then we have a veritable incipient family, though with but one parent. A budding Hydra, a colonial infusorian, show us such an embryo family. In these, as in all families, the career of the single individual is much altered by its life in common with others; much of its freedom is sacrificed.

Two-Parent System: Difficulties Introduced

Animals that require two parents find the matter more complex. Some of the advantages of having two parents we have set forth in Chapter I. But this increases enormously the variety and complexity of life; multiplies by thousands its problems and difficulties; perhaps also its interests and satisfactions. There is added to the life career the problem of finding and uniting with the mate; a problem much more difficult than that presented by the performance of most other functions. It requires specialized structures, specialized functions, specialized reactions. The seeking of the mate becomes one of the chief impulses changing the development and behavior of organisms, playing everywhere a tremendous role. It seems one of the chief bases of structural and mental evolution; it cannot be left out of account, whether we are dealing with the family or with any other product of evolution.

Differentiation into Male and Female: the Problems of Feminism

At its lowest, reproduction from two parents is still carried out in a relatively simple way. In some organisms the individuals simply cast their germ cells abroad, leaving them to unite or to fail, as chance may dictate; leaving the united product to develop as best it may. Such is the situation in many plants, in many aquatic animals. But as the conditions of life become more complex, this does not suffice. The mates seek and find each other. This becomes one of the main features of the life career. A difference arises between the two mates; a difference not present in the lower grades. One does most of the seeking, and carries minute germ cells that move and actively unite with the others. We call this the male. The other, the female, produces and carries large germ cells, in which she stores up food for the development of the young. Here appears the deepest duality of life, the difference of the sexes. The life career in both sexes is much altered by the mode of reproduction, but in the male far less than in the female. The production of the large germ cells, the storing of food within them, the carrying of them, and their disposition—these things form for the female a large part of the business of life. The special problems of feminism begin far back in the animal series.

This is but the first step in a long progress. The life career of the female becomes still more profoundly altered when the egg, even after union with the germ cell from the male, remains attached to the body of the mother, receiving protection and nutrition, till a certain stage of development is reached. We find among animals all stages in this union. In some it goes but a little way. The female carries the egg merely till it is ready to hatch, then casts it abroad. In others the union becomes longer and more intimate, till we reach the conditions found in the group to which man belongs, the mammals. Here the young is long identified with the parent. The new individual is not cast on its own resources until it has reached a rather advanced stage of development.

This intimate union of parent and offspring, for a long period, has large consequences. The development of the offspring is greatly changed. And the parent is modified hardly less; her entire physiology, metabolic, glandular, nervous, mental, is tremendously influenced. In this union of parent and offspring we have another major factor in development and behavior, comparable to that due to the requirement of mating. But this union affects directly but one of the parents, the female. The family at its beginning includes but mother and offspring. The male still retains his freedom, save for the mating requirements.

Economic Dependence of the Female

But the chain binding the male to his mate gradually brings him too under the domination of the developing offspring. His mate is under a heavy handicap while carrying the developing young. Her life career so weighted down becomes inadequate to nutrition and protection. The life career of the male, already greatly modified for the seeking of the female, becomes further changed toward retaining possession of her; toward feeding and protecting her while carrying and guarding the young. This situation we find widespread: in fishes, in birds, in mammals, the male protects and aids the female. The economic dependence of the female has begun.

Parallel with this we find another step. The wide-reaching influence of the young on the mother does not disappear at once on its separation from her body. It remains a source of reaction, an object of interest, after it has become free. The parent from which it has separated continues to protect it, to supply it food, to keep it under conditions favorable to its further development. Complex structures, complex activities, arise in carrying out these functions. The life career is deeply modified. This becomes almost its chief motive. The mother wasp prepares food for the future young, a spider or larva that has been stupefied; deposits the eggs in this. The bird mother builds a nest, keeps the eggs warm, feeds the young. The family has now developed further; but in the simpler cases it still consists mainly of the offspring with but one of the two parents, the female.

Coöperative Career of the Two Parents

But the male too becomes drawn into this work. The female and her behavior have become the strongest source of stimuli for the male. Her concern with the offspring deeply influences him. At times his relation to the progeny appears but indirect. He protects the females; the progeny too are protected. In places it is more direct. The drawing of the life activities of the male into the circle of family life appears, as we survey the animal kingdom, in curious, isolated and unexpected ways. The male catfish of certain species takes the eggs in his mouth and there holds and protects them until the young can care for themselves. Certain male toads take the eggs on their backs and there carry them until the young animals hatch and escape. In various fish the male helps build and guard the nest, and takes part in protecting the swimming young. Some male birds help build the nest; feed the female while she keeps the eggs warm; take their turn at that work; help to feed the young. In some mammals the male concerns himself little or hardly at all with these domestic matters; in others he plays an active role in providing a home and caring for the young.

Along with this intertwining of the life careers of parent and offspring, there come changes in the relation of the two parents to each other. In some animals the relation is but a passing one; the male seeks the female; then after union of the germ cells separates from her; they consort no more; and the next mating will be with another individual, or as chance may direct. But as the development of the young comes to be dependent on the parent or parents, as the parents feed, protect and guide the young, the behavior of each parent becomes correlated with that of the other; they coöperate. The mating relation is continued between the same parents. We find here perhaps two main lines of evolution. In one group, typically each male mates with a limited number of females, which he protects from enemies and defends from other males, incidentally protecting their young. The polygamous family has arisen: the herd or flock, headed by a single male, as in cattle, in seals, in many mammals.

One Male Mated to Many Females

The polygamous family presents biological difficulties. Since in most species the number of males and females is approximately the same, the appropriation of several females by one male results in the exclusion of many males from propagation; results consequently in perpetual war among the males. Since in the nature of the case it is the more powerful warriors among the males that become parents of the next generation, this method of organization results in selective elimination in favor of the warlike; cuts out the pacifists; operates against the development of the virtues of peace; keeps society at war. As might be expected, in such polygamous families the males have little direct concern with the care of the young beyond the protection of the flock as a whole. Their business is mainly fighting, and propagation.

One Male Mated to One Female

But in those more numerous cases where the male becomes directly involved in the business of caring for the individual young produced by a particular mother, coöperation between a single male and a single female becomes the rule. Care of their common young keeps them together; the mating relation continues; successive children may be borne to the same pair. What we usually think of as the family has come into existence: two parents and their offspring living together, carrying on their life careers in unison, sharing nutriment and protection, coöperating in activities. Such families are found in a great number of animals of diverse groups; they are by no means peculiarly a human institution.

Temporary Unions

The duration of the family relation depends much on the length of time that the young are so imperfect as to require assistance, and also in a minor degree, on whether propagation is seasonal. In birds, and in many mammals, mating occurs only at particular periods of the year, and the young are dependent for but a short time; the family then remains a unit only for the same length of time. Then the parents separate from the children, and the two parents part, carrying on independent careers. In some cases, as in pigeons, two successive broods of young overlap; the second one begins before the first has left the parents. In such cases the two parents remain mated, bringing up together two families of young. But at the end of the season they separate, each pursuing his own career, and at the next season each may enter into a family with a new mate.

Life-long Unions

But there exist or arise in many animals powerful biological influences that favor a coöperative career of the parents lasting for more than one season, or for life. The attraction of the mates for each other, combined with the effect of habit, itself acts powerfully in this direction. In the eagles, hawks and other birds of prey this keeps the mates together for life; a permanent monogamous marriage is here found. Successive families of young are produced, and though there intervene periods in which the parents are without young, the union of mates is for life.

In other animals this tendency toward a permanent coöperative life career on the part of the two parents is powerfully reinforced by the long period of dependence of the young. The development of the offspring to maturity requires not one season but many. The two parents, caring jointly for the young, remain together. The offspring come, not in broods, but singly. Succeeding children overlap in their developmental careers. There is no time when the two parents can separate without breaking in upon the functions they have undertaken in relation to the young. Such is the situation we find in the higher anthropoids, in the orang and gorilla; such is the situation found at its highest development in man.

Independent Origin of Monogamous Family in Different Animals

Meanwhile too the life career in such organisms has become full of complex activities of other sorts, requiring for their proper performance the undistracted attention of the individual, and all this is intertwined with the care, protection and guidance of the young. To break the mating relation at any particular time is to bring all this into confusion; is to leave children and mate in distress; is to leave unfilled the mating impulse; is to force the separated mates anew into the intensely distracting pursuit of finding a new mate. All this is avoided by the mates remaining together. Even as age comes on, and the last of the offspring has taken up its own career, so that the biological relations with progeny no longer require coöperation on the part of the parents, long use and habit, the persistence of the need of companionship, keep together the two parents. Marriage is life-long, even though the care of the offspring is not. Permanent monogamous marriage has arisen independently, through similar functional requirements, in the mammals and in the birds; the biological needs giving origin to it being much the more numerous and powerful in the higher mammals. Thus it is emphatically not true, as is so often asserted with assumed finality, that the only function of marriage is the production of children. On the contrary, marriage and the family are a complex resultant from the interaction of many functional needs. The satisfaction of the powerful mating impulse, one of the chief factors in organic evolution, reinforced as it is by many structural and functional complexes that have arisen in connection with it, is one of the major elements concerned. The thwarting of all that is connected with this impulse profoundly affects, and often deranges, the life career. No institution that leaves this function unfulfilled can be considered a biologically adequate one.

Such then is the family as we find it in monogamous birds, mammals and man: a life correlation, a union, of the careers of the two mates, and of both with the careers of the successive children till these are self-supporting. Its chief biological bases, in distinction from other systems found in organisms are—in addition to the fundamental mating impulse and the production of young—the helplessness of the children at first, demanding parental support; the long time required for their development to the period of self-help; the marked handicapping of the female while the children are infantile; the lack in man of the seasonal period of mating and reproduction; the overlapping of the immature periods of the successive children; and the complexity of the individual life career, with the intertwining of its manifold activities with these reproductive relations. The monogamous family, with its life-long union of mates, appears as the final term of a long evolutionary series.

Functions of the Family Taken by Society

But as we examine the varied animal world we find another set of relations appearing, leading to a different culmination. Groups larger than the single monogamous family act together for support and protection. Indeed, the single family itself develops into such a group, when its members remain together after the progeny have themselves reached the period of mating. Still more readily is such a group formed from the polygamous family, of one male with many females; the herd protects itself and all its parts by common action. Society as a whole takes over many of the functions of the family. This situation too exists in man as a supplement to the monogamous family. At a certain period before maturity, the school takes over in certain relations the care of the young.

But this condition cannot readily reach its extreme development—society cannot fully supplement the family—in organisms where, as in mammals, there is a long-continued, intimate union of offspring with parent, during which the child is brought to a considerably advanced state of development. Society cannot take over *this* parental function. And by that long and intimate union both parent and offspring are so fundamentally modified, in structural, physiological, and mental constitution, as to place great obstacles in the way of society's assuming control of the children even soon after birth.

It is in organisms not showing this intimate union of parent and offspring that we meet most highly developed this exercise by society as a whole of the functions taken elsewhere by the family; it is in certain of the insects that we find the culmination of this system. In these social insects the two parents play little part in life save in the production and bringing together of the germ cells. The life of the species—the individual life careers—is carried on by individuals that are not parents, non-sexual individuals. Such is the situation in some of the ants, in some of the bees, in termites. In social organization these have, as William Morton Wheeler [3] has brought out, passed to a stage in evolution much beyond that of man; though whether for better or worse is another question; and it is another question too whether this is a line of evolution that man can or must follow. In these ants and bees the functions of the parents have become purely propagatory; beyond this they have practically no life career. One female in the state is selected as mother. She is fostered and fed and protected for the young she produces; the other females are destroyed or transformed by special treatment into non-sexual individuals. The males as such play a role only in that one of them fertilizes the single group-mother; after one has done this, all males may be destroyed, as in the bees, or in other cases they too are transformed, like the females, into neutral individuals. Society is non-sexual; carried on, not by husbands and wives, fathers and mothers, but by neuters. The whole distracting business of mating, of marrying and giving in marriage, is cut out of these societies; the individuals can apply themselves whole-heartedly to their life careers. The young produced by the group-mother are cared for by certain of these neutral workers who make this their life business. The family does not exist; it is a state in evolution that has been left behind, transcended. The attainment of some such situation appears to be the aspiration of certain groups of men.

Such then are perhaps the chief types of situations that we find in organisms as the result of the interaction of reproduction and the other business of the life career. One main line of development culminates in the monogamous family, as found in birds, the higher anthropoids, and man; the other in the highly organized society without families, found in the social insects.

Systems Found in Man

When now we turn to a closer examination of the situation in man, we discover that here, as in so many other relations, man forms, either in concrete realization or in tendency and aspiration, a sort of abstract and brief chronicle of the entire biological series. In the main perhaps he represents the fully or incompletely developed monogamous family. But we find too, scattered in the highly differentiated groups of mankind, a number of the diverse phases that occur in the different groups of animals. Man cannot indeed go back to the phase of mere isolated individuals; the mother at least is for a long time actually physically identified with the child; and even after the child has left her body she is held almost as powerfully united with it, though in a different way. But the male is, in man as everywhere else, less identified with the offspring; and there occur scattered individuals who tend to revert to the ancient type in which the males serve, in the work of reproduction, merely as fertilizers of the egg, leaving the rest of the work of the family to the female. These seem to be but sporadic throw-backs. Biologically they cannot be considered adequate members of society; at least not until society becomes organized on some such plan as we find in bees and ants, making the males largely superfluous. There exist species of animals in which this otiose and incompetent condition of the males has developed far; in which (as in rotifers) the males are but a few short-lived dwarfs, without life career aside from propagation. It is not true, as is sometimes asserted to be the case, that the male must in the nature of things be more powerful and efficient and self-assertive than the female. On the contrary, in many animals the male is the weaker vessel, even rudimentary; to the point, in some species, of complete extinction, leaving the species to consist only of females. In an entire subdivision of the Rotifera we find this situation. In organisms in which there is sex, the female is indispensable, while the male is not; the female can carry on the race alone, and in some species does so.

Partial Development of the Family

More widely occurring in man than this tendency of the male to abdicate his role in the family are certain phases of partial development of the family. There exists in man the condition in which the single male possesses several or many females and acts as the head of the entire complex group; a condition found in many mammals of the cattle kind, as well as in others. There occur in man also situations hardly found in other animals; as that in which the female has a definite and limited number of husbands; also various combinations or modifications of these two systems. Systems of this sort cannot prevail without excluding many individuals from propagation, with the consequent distraction and warfare that this brings. The polygamous system is sometimes defended on the ground that it is the stronger, more warlike males that become the parents of the next generation, the weaker ones being excluded; a measure that is held to be of eugenic value, resulting in continued selection and consequent steady raising (in a certain direction) of the level of the population. But whether this notion is sound or unsound, the tendencies of the human race appear distinctly against this condition and it seems certain to disappear; it yields disturbances, distractions, and other consequences that are felt to be intolerable. The monogamous family appears at present the system of greatest stability in man, though itself with irregularities and unstable points.

Temporary Families: Difficulties

Another system proposed for man, and to some extent practiced, is that of temporary families, such as we find in many birds and other animals. Individuals are to become mated for a longer or shorter period, separating as they please. This system, unless supplemented in some radical way, ignores the long period of dependence of the children on the parents; the result of which is that the frequent separation or change of mates gives serious wrenches to the framework of society; injures the children, distracts and distresses the parents. Such a system, therefore, cannot be held to meet adequately the difficult problems of the relations of parent and offspring; cannot be considered an efficient system for smooth social working, for peace and prosperity. If defended it must be by the extreme selectionist who holds that severe and unfavorable living conditions, with a high death rate, are in the long run advantageous to the species. If combined with the prevention of the production of offspring, as often proposed, and as seems indispensable if it is not to give rise to immediate distress and dislocation, it must result in the extinction of the species; or else it must prevail in only part of the population, another part living under some system adequate to the care of the offspring.

Abolition of the Family; Biological Consequences

In some quarters we meet an aspiration for a system showing the essential features of that found in those insects whose social organization has advanced so far beyond our own; a system in which from the beginning the social group as a whole shall care for the offspring, thus making the family unnecessary. In this way the individual parents are to be relieved; set free each to pursue his or her life career without interference from offspring or mate. As we find it in popular modern proposals, this aspiration appears largely dominated by the desire to set free and give full satisfaction to the mating impulse; to facilitate change in mates, making it unnecessary for them to remain tied to one another longer than fancy dictates. If we examine this aspect of the matter in the animals that have fully carried out this system of public care for the progeny, we find a surprising result. The system has resulted, not in the freeing of the mating impulses, but in their suppression; their almost complete extinction; in the essential desexualization of society. Only a few isolated individuals continue to be occupied with mating and propagation; the rank and file are sexless. If man must look to this result, possibly the enthusiasm for this system will abate.

Monogamy as the Outgrowth of the Biological Situation in Man

Indeed, it appears that man must meet a very great difficulty in inaugurating any thorough-going system of social care of the offspring, through the fact that he has already made extensive progress in the opposite direction; in the direction of care of the offspring by the immediate parents; through the fact that he is a mammal instead of an insect. In the insects the mother has never been long and intimately identified with the offspring until it is far developed, as is the case in man. That long and intimate physical union has modified all the characteristics of the human mother and through her those of the species as a whole; for inheritance occurs in many respects from one sex to the other. In man, separation of parent from offspring is impossible for a long period, and if hurried even after physical union has ceased, it may turn out that this will lead to serious injury to parent and offspring. To discover the proper period of separation of the lives of the two is a matter for observation and experimentation; not for the application of *a priori* principles.

It may indeed be questioned whether man has not been too late in starting on a radical plan for the supplanting of the family by society as a whole. To make a thorough success of this, he should have begun it æons ago, before he became a mammal. In that case by the present time he might perhaps hope to rival the ants in social organization.

A valiant and venturesome attempt to meet this difficulty lies in the suggestion of J. B. S. Haldane in his booklet on Science and the Future;[4] and Charlotte Haldane[5] has pictured for us society as it may be after the plan is carried out. The human germ gland is to be artificially and impersonally cultivated in isolation by modern methods of tissue culture. The germ cells are to be likewise developed from the start in public incubators; these to be followed by other public institutions for later stages, till development and education are complete. Such a proposal helps to visualize the very great biological difficulty involved in the attempt to (now) change the direction of evolution in man; to reverse the long course he has traveled toward the family system; to transform him from a mammal into something else; to start him on a course leading to replacement of the family and the parent by society as a whole. Evolution is never closed; and what man may become through millions of years of effort in that direction no one can say. But certainly a long and hard road would have to be traveled before that plan could be made a success. The varied difficulties offered by the present nature of man: the fact that he is a mammal, his long and helpless infancy, the high development of his mating and parental impulses, and his diversified and exacting life career, appear to be met more adequately (though obviously still imperfectly) by the lifelong monogamous family than by any other system. Doubtless experimentation with other systems will continue; and there can be no certainty as to what the future may bring forth. But it is the present nature and needs of man that have led to the establishment of the monogamous family, and there appears little likelihood that this system will soon generally be superseded by another.

NOTES AND REFERENCES ON CHAPTER XI

1. Page 253. See Ben B. Lindsey, *The Companionate Marriage* (New York, 1927), and the extensive discussion to which it has given rise. Dr. John B. Watson, founder of radical Behaviorism, entitles an article "Men Won't Marry Fifty Years from Now," and in the course of it demands "Who started this business of monogamy, anyhow?" (In Hearst's International Magazine for June, 1929.)

For more conservative points of view see *Family Life To-day,* edited by Margaret Rich (Boston, 1928).

2. Page 253. Details regarding the social relations of animals, including those leading up to marriage, will be found in Fr. Alverdes' *Social Life in the Animal World* (New York, 1927).

3. Page 263. See Wm. M. Wheeler, *Social Life Among the Insects* (New York, 1923); also by the same author, *The Termitodoxia, or Biology and Society,* The Scientific Monthly, February, 1920, pp. 113–124.

4. Page 267. J. B. S. Haldane, *Daedalus or Science and the Future* (New York, 1924), 93 pp.

5. Page 267. Charlotte Haldane, *Man's World* (New York, 1927).

XII

RACE MIXTURE AND ITS CONSEQUENCES

IN America, and in many other parts of the world, mixture of diverse races is occurring on a vast scale. What will be the consequences? Is race mixture harmful? Must the results be bad? Or may the results be good? Is the "melting pot" a glorious experiment, filled with hope for humanity? Or is "the melting pot a myth"; its results bound to be disastrous? What does biological science know of the consequences of mixing races?

What Are the Results of Race Mixture?

Biology has gathered through experiment much positive knowledge on the results of intermixing diverse types of organisms. The extensive knowledge of the genetic system—of the chromosomes and genes, and of their method of action (set forth in earlier chapters)—provides a solid foundation for understanding the effects of mixing diverse races. And an immense number of experiments on this very matter have yielded definite results, have brought to light many important consequences of mixing races.

Race mixture consists essentially in putting together, into single individuals, genes that were before in separate individuals of diverse types; putting together genes that separately yield very diverse results. What consequences follow?

Results When Very Diverse Organisms Mix

If the organisms from which come the two sets of genes are very diverse, the results may indeed be disastrous. In nature, the genes of a clam or an oyster never unite in the same individual with those of a sea urchin or a worm, for the chromosomes of the one will not enter the egg of the other. But Loeb discovered how to circumvent nature in this respect. By chemical treatment he caused the egg of the sea urchin to be fertilized by the sperm of the worm, or of other very diverse animals. But this meant destruction to the chromosomes and genes that entered the egg of the strange species. The protoplasm of that strange species is poisonous to them; under the microscope the foreign chromosomes are found to fade away and disappear. The sea urchin egg fertilized by the worm or mollusk or the starfish produces a sea urchin pure and simple; the foreign genes have had no effect on the offspring. In wide circles this is the effect of crossing distant species; their protoplasm and genes are incompatible. The egg of each species permits the development only of genes of its own type.

But if the diverse organisms are less distant in relationship, only a part of the foreign chromosomes may be destroyed. Some of their genes resist the attack of the strange cytoplasm. These take part in development; individuals are produced that in the main are like the mother, but show also a few characteristics of the father. When different species of sea urchins are crossed this is commonly the result. A part of the chromosomes of the father are seen to fade away in the egg; others remain and influence the offspring.

Incompatibility of Chromosomes

In many of the crosses between species not distant, some chromosomes from both parents are destroyed. The genes of each parent appear to be poisonous to most of those of the other parent; yet some from each parent survive. Then the egg begins to develop. But soon it stops; the young organism dies. Curiously, if all the chromosomes of one of the parents are completely put out of operation, the egg may develop in its usual way, producing offspring that are like the other parent. But when there is less antagonism, so that some (but not all) of the chromosomes of both parents survive, the injury is greater, and death occurs before development has gone far. A single full set of chromosomes is efficient, but if with it are combined fragments of another set, or if neither set is complete in itself, the result is usually confusion and death.

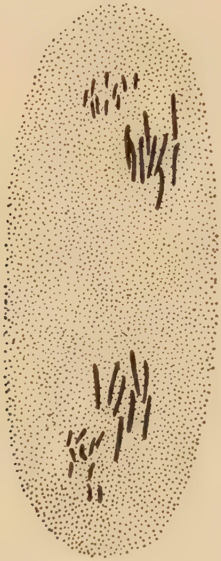


Figure 46. Egg about ready to divide, formed by crossing two species of fish (Menidia by Fundulus). The two kinds of chromosomes are grouped separately; the long ones are from the Fundulus male; the short ones from the Menidia female. Enlarged from a figure by Moenkhaus (1904).

Tennent[1] observed in crosses between different sea urchins many cases in which part of the chromosomes from each parent were destroyed.

Sometimes the set of chromosomes from one parent is very different, in the size of the chromosomes and in their number, from the set from the other parent. Then in the egg the two sets may remain separately grouped (figure 46), and development may begin. The chromosomes of both sets divide, and pass into the new cells formed. At the same time they begin to intermingle. But it turns out that they cannot work together. Soon development goes awry; the young creature becomes deformed, abnormal, and soon dies. The action of one of the sets of genes is incompatible with that of the other, and the individual that forms their battleground perishes.

Of closely related species, it is generally true that two whose chromosomes are much alike in size and number may cross and produce well-grown young, while if their sets of chromosomes are very different, their young cannot develop. In the much studied fruit-flies, the two species Drosophila melanogaster and Drosophila simulans have chromosomes that are much alike (figure 47, A and B). These two species can produce hybrid young, while neither of them can produce offspring when crossed with Drosophila virilis (figure 47, C), which has a very different set of chromosomes.

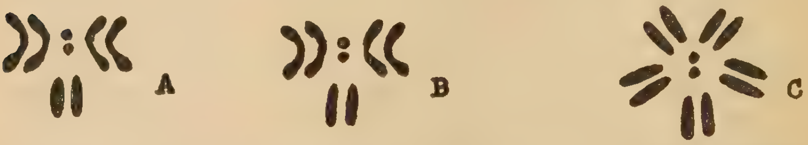


Figure 47—Chromosomes of three species of Drosophila. A and B, the similar groups of eight chromosomes in Drosophila melanogaster and Drosophila simulans; these two species can be crossed. C, chromosome group of Drosophila virilis, with twelve chromosomes in place of eight; this species cannot be crossed with the others. After Metz, Moses and Mason (1923).

Sterility

Yet there are many cases in which two diverse sets of chromosomes, from parents of different species, work perfectly together in producing immediate offspring, but will not work for the production of later generations. In the development of the young of the first generation, the two sets of chromosomes need not come into the closest possible relations; therefore they do not injure one another, and vigorous, well-formed young are produced, having the two sets of different chromosomes in all of their cells. Such is the case in the production of the mule from the ass and the horse. But when these young have become adults, and proceed to form germ cells of their own, the two sets of chromosomes refuse to operate together, so that no germ cells are formed, and no offspring are produced. In the production of germ cells, the chromosomes from the two parents come into much more intimate union than in the mere development of the individual. In forming germ cells, each chromosome from one of the two parents mates closely with the corresponding chromosome from the other parent, becoming intimately united with it; then the two separate into different germ cells. But if the two parents have different numbers of chromosomes, then the mating of corresponding chromosomes cannot occur, or cannot occur fully and perfectly. Always certain chromosomes are left unmated. These unmated chromosomes are distributed irregularly to the germ cells, so that the latter are abnormally formed. In place of having one chromosome from each pair, the germ cells get irregular and unequal combinations of chromosomes and genes. In consequence they cannot function properly; usually they die without uniting with the germ cells of another individual. The individuals that form such abnormal germ cells therefore leave no offspring. The mule is a familiar example of this. Its father, the ass, has 64 to 66 small chromosomes; its mother, the horse, has 38 large chromosomes. The mule, receiving half of these from each parent, has about 51 chromosomes; 19 large ones from the horse, 32 or 33 small ones from the ass. These can work together to produce the robust mule. But they cannot pair normally to form germ cells; so the mule has no offspring. Many crosses between different species are thus sterile.

In many such crosses between different species, while most of the germ cells produced are abnormal and inactive, a few by chance receive combinations of chromosomes and genes that enable them to live and to unite with other germ cells. Such hybrid individuals may therefore produce a very few offspring. Every possible grade of complete or partial sterility is exemplified in different hybrids, up to cases where the hybrids are completely fertile. That is, the genes and chromosomes of different species or varieties show all possible grades of incompatibility, from complete inability to work together, up to cases in which normal and fertile offspring are produced.

Incompatibility of Structures and Functions Resulting from the Different Genes

In a large class of crosses, the chromosomes of the two parents work very well together, in the sense that they do not poison or destroy one another, nor refuse to mate; yet the individuals produced are imperfect or abnormal. This is because the two different sets of chromosomes tend to cause development in different directions. One works toward the production of one set of structures and functions, the other toward another set. Something of this kind occurs, as we have before seen, in almost all cases in which offspring have two parents; the two sets of chromosomes tend to produce different individuals, and the result is some sort of a compromise. But when the parents are very different, a workable compromise is not possible. Structures are produced that will not operate together, or that will not properly perform certain required functions.

Disharmonious Combinations

An example of this is seen in the cross made by Newman [2] between two common species of small fish, belonging to the genus Fundulus. One of these is larger than the other. The large species produces a larger egg, containing more yolk than does the egg of the smaller species (figure 48, A and B). In the development of each species, the large egg develops more slowly than the small one, but after the circulation of the blood is set up, the heart beats oftener and blood circulates more rapidly in the large species than in the small one. The result is that in the large species the yolk is now rapidly absorbed by the blood, so that when the young fish is ready to begin swimming about, the yolk has disappeared and the fish can become active. When now the egg of the larger species is fertilized by the smaller one, so that the new individual contains a set of genes from both species, development begins as usual, and a young fish is formed on the surface of the large egg (figure 48, C). But as a result of the presence of the genes from the smaller species, the heart-beat and circulation of the blood are slower than usual. In consequence the abundant yolk of the large egg is not absorbed so rapidly as is required. When therefore the young fish has reached the stage in development at which it should begin to swim about, it still has a large mass of yolk attached to its body (figure 48, D). This proves an obstacle to its swimming, it is unsuccessful in making its way about; weighted down by its mass of yolk, it dies. One of the parents had brought it a large

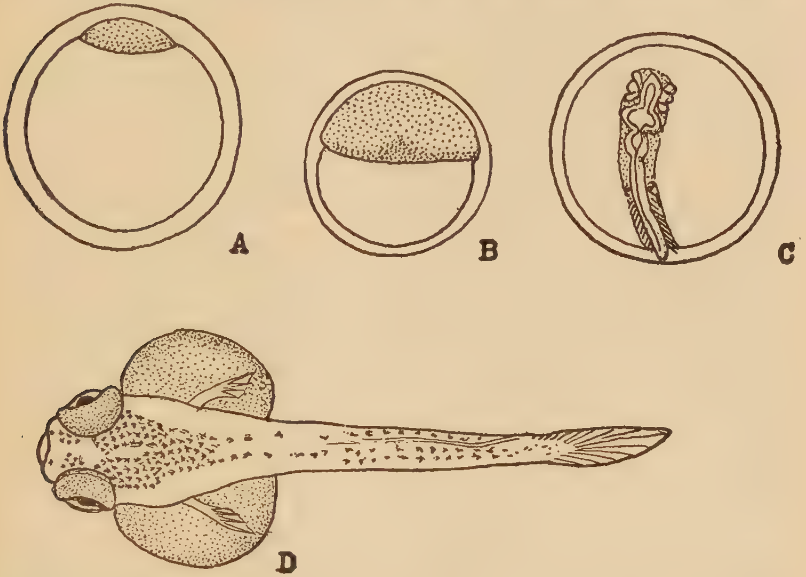


Figure 48—Development of a hybrid between a large and a small species of fish, Fundulus. A, egg of the larger species; B, egg of the smaller species. C, young fish developing on the egg of the larger species, after fertilization by the smaller species. D, the young hybrid fish at the time at which it should begin to swim about. A large mass of egg yolk still remains, preventing successful swimming, so that the hybrid dies. After Newman (1908).

mass of yolk; the other a slow heart-beat and circulation. This combination is inharmonious; it results in inefficiency and death. In another way also Newman found that the mixed individuals were less efficient than the pure ones. He tested the resistance of the young developing fish to carbon dioxide. The mixed individuals were less resistant than the pure individuals of either species; they were killed by a weaker concentration of carbon dioxide.

Thus in several ways the mixed individuals were less efficient physiological machines than the pure ones. The structures and functions resulting from the two different germ cells that are united form a combination that does not work harmoniously. There are great numbers of cases of this sort, in which the characteristics coming from the two parents are inharmonious. The consequences range, in different cases, from early death, through conditions of abnormality and deficiency, up to mere awkwardness, or stupidity of behavior. Some cases of these latter types we shall mention later.

Dangers and difficulties therefore abound in the intercrossing of parents that are markedly diverse, in the union of individuals whose genes have different effects.

Harmonious Combinations

But the nature of the consequences depends on the nature and degree of difference between the genes, and between their effects. In organisms that reproduce from two parents, as do man and the higher animals and plants, practically every individual differs in some of its genes from every other. Yet reproduction nevertheless continues to occur with success. The union of two somewhat different parents to produce offspring has indeed many advantages, as we have seen in earlier chapters. Often one parent, or both, carries imperfect genes, that taken alone would result in defective offspring. The union of two is therefore a method of insurance; a device by which the frequency of getting at least one good gene to each pair is greatly increased. The mating of two slightly diverse races often gives offspring that are superior to either race. The chromosomes are not sufficiently diverse to poison each other; the structures produced are not incompatible, but instead are supplementary. The offspring therefore excel the parent in vigor and efficiency. Chapters I and X may be consulted for this method of action. Intermingling of the genes of diverse parents may result, therefore, either in injury or in improvement, depending on the degree of diversity of the parents, and on the particular types of genes that the two parents possess.

The Situation in Man

What now is the situation in the crossing of diverse races of man? What are the results of intercrossing among the diverse races that come to us from Europe; among Germans, Celts, Slavs; among Nordics, Alpines and Mediterraneans? What are the biological consequences of intercrossing between whites and blacks; between Europeans and Asiatics; between Europeans and American Indians?

Are the differences between the races of man so great that there is incompatibility between their genes, their chromosomes, as is the case for many mixtures of types in other organisms? Are there differences in the structures and functions produced in the different human races by the genes, so great that the combination of two races is inharmonious, resulting in injury and inefficiency? Or finally, are possibly the genes of diverse races supplementary, so that some or all of the offspring of a cross may be superior to the parent races? Of all these conditions we find examples in other organisms.

We shall take up these possibilities in series. And first we shall deal only with the effects of race mixture irrespective of the question whether certain human races should be considered superior to others. This latter question is reserved for consideration in later paragraphs.

No Incompatibility of Chromosomes in Man

No incompatibility of chromosomes is to be observed among the different races of man. The negro and the white man each has 24 pairs of chromosomes. These work perfectly together, both in forming vigorous offspring, and in the much more delicate test of later uniting to form germ cells in these offspring. The same is true for crosses between any of the other races of man. If injury to certain genes or chromosomes occurred, this would result in abnormal structures or functions, such as we see in other organisms; or in abnormal ratios of one sex to the other; or in partial or complete sterility of the offspring of crosses. Nothing of the sort is to be observed. With respect to the main features of physical structure and of physiology, the offspring of parents belonging to diverse races are as perfect and vigorous and efficient as the offspring of members of the same race. We may dismiss from consideration, so far as crosses of human races are concerned, the question of serious incompatibility of chromosomes or genes, such as we find in crosses between organisms standing far apart in their structure and physiology.

No Incompatibility of Fundamental Structures and Functions

It is further true that in their chief features, the later structures and physiological functions resulting from the genes of one race of man are not incompatible with those from the genes of other races. The two sets of structures and functions can unite in a single individual that is an efficient physiological machine; at least with respect to the great biological functions involved in nutrition, respiration, nervous action, reproduction and the like.

Is There Disharmony in Details?

But there remain certain questions of detail, some of them important. May the structures and functions of diverse races be so different in details as to give crosses that are at a disadvantage as compared with the parents? In particular, may there be features of mentality, of behavior, in which mixed individuals are inharmonious, as compared with those of a single race? Lack of harmony even in slight degree in these matters may lead to serious consequences.

What Is the Race?

In considering such questions, it is important to remember that the individuals of any so-called race differ greatly among themselves, in their genes and in their consequent developed characteristics. A "race" in man is merely a group of individuals having many genes in common or much alike, though also with many diverse genes among the component individuals; and differing with respect to their common genes from other groups of individuals, other races. No race is uniform in its genes. Within every race therefore, mating of diverse individuals yields many types of results, of the sort set forth in Chapter I. Some matings result in the production of offspring that are inferior as compared with the parents; others in the production of superior offspring. Even within each race, reproduction is a process of continual formation of new combinations of genes, some more efficient, others less. Results of all these diverse kinds must therefore be expected also when the parents are members of diverse races; and they certainly occur.

But do race crosses show this sort of thing in any greater or less degree than individuals of a single race? Are there characteristic differences in respect to any of these things, when we compare populations of mixed individuals with those formed from a single race?

Two classes of characteristic differences there are. One results to the advantage of racial crosses, the other to their disadvantage.

Advantages of Race Crossing: Hybrid Vigor

To the advantage of race crosses is the fact that any defective genes present usually will not be found in the same pairs in the two races. In view of the immense number of genes carried by individuals of each race, and their separate history up to the time of the cross, the relatively few defects that have arisen are almost certain to affect genes of different pairs in the two. Hence when the races cross, the individuals produced will receive a normal gene from one parent or the other in most of their gene pairs; and since the normal gene usually manifests its effect, the offspring of the cross will have fewer gene defects than either of the parents. This, as is well known, is what occurs in the crossing of diverse races in many domestic organisms; the offspring are superior in vigor and in other respects to either parent (see Chapter X). This "hybrid vigor" has been observed in crosses between diverse human races. Fischer[3] found that the offspring of Boers and Hottentots in South Africa are on the average greater in stature than either parent race, notwithstanding the fact that the Hottentots are much below the Boers in stature. But the manifestations of this greater vigor in hybrids are probably lessened owing to the fact (to be taken up next) that in certain details the characteristics of the two races may be inharmonious. On the whole, increased hybrid vigor has not shown itself in a very marked way, in the crosses thus far studied between different races of man. But the crosses are by no means, on the average, less robust than the parent races.

Disadvantages: Lack of Harmony in Details

Working probably to the disadvantage of some race mixtures in man is the fact that certain human races differ in such ways that union of their characteristics may yield combinations that are in details inharmonious. In the mixture of races found in the United States, as Davenport[4] has pointed out, some of the stocks differ greatly in physique from others. Some are smaller, having organs that go with a small body—small heart, small kidneys, small jaws, small teeth; such on the whole are the races that come from the Mediterranean region of Europe. Others have large bodies, with large kidneys, heart, jaws, teeth, and other organs.

Judging from what occurs in other organisms, when such diverse races are crossed, the offspring, receiving genes from both sides, may well develop combinations of parts that lack complete harmony. If a large body is combined with small kidneys, the latter may be insufficient for the needs of the individual. Or a large body might be combined with a small heart that would not keep the blood properly circulated. Large teeth, resulting from the genes of one parent, may be crowded in a small jaw that results from the genes of the other parent.

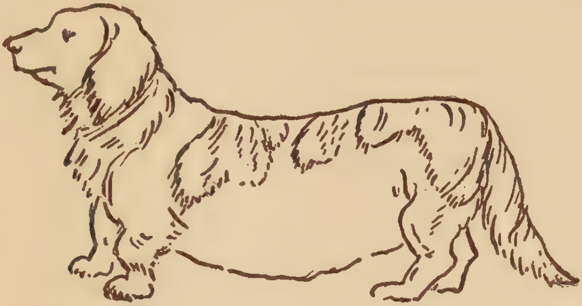


Figure 49—Cross between a Great St. Bernard dog and a dachshund. After Lang (1914).

In consequence the teeth decay. Partly to it, Davenport (by whom the examples given above are suggested) ascribes the prevalence of defective teeth in the United States. According to him, crowded and defective teeth are less common in nations with races less mixed.

It is difficult to measure with certainty lack of harmony, between body size and size of kidney or heart, so that direct proof that the possible inharmonious combinations mentioned above actually occur in man as a result of mixture of races is not available. But the occurrence of inharmonious combinations of certain bodily parts as a result of race crossing has been observed both in man and in other organisms. A striking case of this kind in the dog—comic rather than tragic in its consequences—is described by Lang.[5] A Great St. Bernard dog was crossed with a dachshund. Some of the progeny had the large heavy body of the St. Bernard, resting on the short crooked legs of the dachshund. The result (figure 49) was neither beautiful nor efficient.

The occurrence of inharmonious combinations, in human race crosses, has been shown with respect to parts of the body that are measurable, in the recent study made by Davenport and Steggerda [6] on the whites and blacks in Jamaica, and on the browns resulting from crosses between them. The whites have relatively short legs and long bodies, while the blacks have relatively long legs and short bodies. "Some of the mulattoes have an unexpected combination of long legs and long body and others of short legs and short body" (Davenport). Again, in the blacks, arms and legs are both long; in the whites, both are shorter. Some of the crosses have "the long legs of the negro and the short arms of the white, which would put them at a disadvantage in picking up things from the ground."

Since inharmonious combinations of physical characteristics that are thus open to precise study are shown to occur as a result of race crossing, it appears probable that similarly inharmonious combinations of a more serious character may likewise occur, giving rise to insufficiency of heart or kidneys, or to crowding of teeth, as suggested in a former paragraph. As we saw earlier, disharmony with respect to such vitally important parts certainly occurs in crosses between different species of fish.

Favorable Combinations

But favorable combinations may result from race mixture as readily as unfavorable ones. Just as some of the crosses may omit the valuable points from both races, combining the poorer ones, so others may combine the valuable features from both. Crossing is practised on a large scale by breeders, for attaining just this result. From one race of wheat may come a high yield, from another a high resistance to cold. By crossing, these features are united, in some of the individuals. In others they are not united; such individuals are discarded from further propagation. Such improved combinations may be produced for all sorts of physical and physiological characteristics, yielding individuals that are more efficient physiological machines than either of the parent races. But always these favorable combinations are accompanied by many unfavorable ones, which must be eliminated, so that succeeding generations consist only of the descendants of the favorable combinations.

Mental Characteristics

Has race crossing similar effects on mental characteristics, on behavior? In animals it has. It may result in combinations that are inharmonious in their behavior. Davenport[4] describes a case of this sort. A white Leghorn fowl was crossed with a Brahma. The white Leghorn is a continuous layer; it does not interrupt the laying of eggs to brood them and hatch young. It is efficient as a producer of eggs, but not as a bringer up of young chicks. The Brahma, on the other hand, produces eggs for a time; then at intervals ceases and broods the eggs till chicks are hatched. It is a careful parent, caring for the chicks until they are ready to shift for themselves.

When the two are crossed, the offspring partake of the characteristics of both parents. It produces eggs for a time; then, like its Brahma parent, ceases to lay, and broods the eggs till they hatch. But then appear the characteristics of its Leghorn parent. It cares for the chicks only a day or two, then abandons them, and goes back to the production of eggs. Its chicks perish. The combination of characteristics results in behavior that is not efficient.

New combinations of mental characteristics with physical ones have been described by Lang[5] in the dog, whose differentiation into diverse races so much resembles that of man. Two varieties of the shepherd dog were crossed. The first was tailless, and gentle and timid in disposition. The second possessed a long bushy tail, and was very lively and aggressive. Among the descendants, one had a long bushy tail, like the second variety, but a timid and gentle disposition, like the first variety. Others had very diminutive tails; some of these dogs were gentle and timid; others lively and aggressive; others showed mixed behavior.

Do Races Differ Mentally?

Does race crossing result in new combinations of mental characteristics in man? This raises the question whether human races differ mentally; if they do not, crossing of races cannot well induce new combinations of mental characteristics. A race, as before remarked, is a set of individuals having many genes in common—in spite of many differences in genes among the component individuals—and differing in these common genes from other sets of individuals, other races. The diversity of genes in different races indisputably yields great differences in physical features—in color, stature, structure, form, and the like. Among individuals belonging to the same race, diversity of genes produces differences in all these respects; and moreover produces differences in mentality; produces differences in power of adjustment to conditions met.

It would be surprising if the same were not true for the differing genes of different races. It might well be anticipated that the European whites and the African bushmen would differ in mentality as they do in physical characteristics. Certainly there is no antecedent presumption against mental differences between different races; on genetic grounds the presumption is that such differences will be found.

Here of course the final word is for observation and experiment. Observations adequate for comparison of human races are difficult to obtain; the number of variable quantities is very great. The intelligence tests made on the army recruits during the Great War indicate, so far as they go, that there are differences of mentality among the representatives of the different European races or nationalities.[7] The comparisons of the blacks and whites of Jamaica, made by Davenport and Steggerda,[6] have the advantage that the representatives examined from the two races were of similar station and lived under similar conditions. These comparisons gave marked differences in mentality between the two races. These may be summarized as follows:

The blacks showed superiority to the whites in the various matters on which depend musical ability; in discrimination of pitch, tone, intensity, and rhythm. They also showed superiority in simple mental arithmetic, and in following complicated directions for doing things. On the other hand, the whites showed a distinct superiority in the tests of intellectual ability. They were superior in copying geometric figures; in making without pattern a drawing of a man; in reconstruction of a manikin; in the criticism of absurd sentences, and in the making of practical judgments. Davenport and Steggerda sum up with the statement:

"It seems to us the outcome of the present studies is so clear that they put the burden of proof on the shoulders of those who would deny fundamental differences, on the average, in the mental capacities of Gold Coast Negroes and Europeans."

Both the genetic situation and the state of the present evidence then indicate that there are characteristic differences in mentality between diverse races. Crossing between two races should therefore give rise to diverse combinations of mental characteristics, some of which will be inharmonious, others harmonious. Davenport and Steggerda believe that this is the situation revealed by their study of crosses between the blacks and whites in Jamaica. The browns resulting from these crosses show inharmonious mental combinations more frequently than do the parent races. "Such disharmonies are apparently more common to the adult Browns. Such disharmony and confusion apparently appear in visualization and reproduction, as in putting together the parts of a manikin. The proportion of failures in the Browns is 9.6 per cent, as opposed to 3.1 per cent in the Blacks and 2.1 per cent in the Whites." "One gains the impression that, although on the average the Browns did not do so badly, there was among them a greater number of persons than in either Blacks or Whites, who were muddled and wuzzle-headed." On the other hand, there were some individuals among the Browns that were superior in certain respects to both Blacks and Whites. Davenport[8] sums up the matter as follows: "In four of the eight Army Alpha tests the browns seem to be inferior to both the blacks and whites. These are all important tests of mentality and lead to the conclusion that, on the average, the browns are frequently inferior in mental tests, while they show more extremes of excellent and poor performance than the other groups."

Are Certain Races Superior?

Judgments of the significance of these results are complicated by the question whether certain races are to be considered superior, others inferior. Judgments of superiority and inferiority must of course rest on relative fitness for certain purposes, on relative efficiency in certain operations. Decision of such a matter is bound to depend on what purposes and operations are under consideration. Objection is therefore sometimes taken to raising at all questions of superiority or inferiority. This however is certainly an over-refinement of scrupulosity. There are many differences in efficiency that all will agree signify superiority. Feeblemindedness is inferior to normal mind; blindness is inferior to sight. In general, higher degrees of sensory acuteness are superior to lower degrees. In general, greater power of adjustment to conditions met is superior to lesser power of adjustment; intelligence is superior to stupidity. And indisputably, differences in all these respects are found among human beings; they may therefore be found, on the average, as between races. The studies of Davenport and Steggerda indicate, as we have seen, that there are indeed differences in efficiency between whites and blacks. The blacks studied were superior in the matters that affect musical ability; the whites in matters of judgment, of adjustment to conditions.

So far as there are differences of superiority and inferiority between races, these differences become, for the races concerned, the all-important fact in race mixture. To the superior race, admixture with the inferior one is adulteration; it means a lowering of quality. All other biological considerations give way to this one. Where one race is superior in certain respects, another in other respects, all depends upon the relative worth of the features in which one or the other race is superior.

Race Crossing and Social Systems

The immediate consequences of race crossing, whether for good or evil, often depend on diversity of social systems in the two races. If the two races have very diverse social systems, as have Americans and Asiatics, as have Europeans and American Indians, the hybrid individual does not fit either system; he is rejected by both. This places him in an unfortunate situation. But this need not mean that he is essentially unfit, as compared to the single races. If such hybrids could start even with members of the single races, each developing his own social system, possibly that produced by the hybrids would be as valuable as the others. But coming into a world in which social systems are already established, the hybrid between races whose social systems are diverse is at a serious disadvantage. Such difficulties are, however, from the point of view of biology, very transitory, though they may be serious while they last.

General Result of Crossing: New Combinations

Where mixture occurs among races which, though different, do not show marked superiorities and inferiorities in important respects, and under circumstances in which the hybrids are not at a lasting social disadvantage, we have the situation exemplified by the mixing of European races in the United States. In such cases the consequences result mainly from the fact that the diverse racial characteristics appear in many new combinations. Some of these combinations may be inharmonious, disadvantageous. Some of them manifest the combined poorer qualities of the races concerned. Others show the combined better qualities of different races, giving rise to superior individuals. All these things will occur for physical and physiological characteristics; and also for mental characteristics. Some of the hybrids will be poorer physiological machines than either parent race; some will be better. If one race has greater activity and energy, the other artistic ability, some of the offspring may have both; they are geniuses. Other offspring will get lack of energy from one race, lack of artistic ability from the other. A population derived from a mixture of races having diverse characteristics will be much more heterogeneous than a population from a single race. There may be better combinations, and worse combinations, than are found in the single races. There will certainly be many individuals showing combinations of characteristics not found in the original races. In the long run there is selective elimination of the inefficient combinations, so that finally a race emerges that is again relatively homogeneous, combining characteristics from all the original races. This process has been gone through many times in the past; through it have arisen the races of the present day.

If the selective elimination that occurs is based on efficiency, it may be hoped that the race finally emerging will be superior to any one of those entering into the combination. But such a consummation will require a long period of time. And in the interval, while the poorer combinations are still present and in process of elimination, the mixed race may expect a lively and varied history. A nation composed of races in process of mixture will not be among those happy peoples whose annals are vacant.

NOTES AND REFERENCES ON CHAPTER XII

1. Page 271. D. H. Tennent. *Echinoderm Hybridization.* Publication 132 of the Carnegie Institution, 1910. In this paper will be found references to other publications on this matter.

2. Page. 274. H. H. Newman. *The Process of Heredity as Exhibited by the Development of Fundulus Hybrids.* Journal of Experimental Zoology, Vol. 5, 1908, 503–561.

3. Page 280. E. Fisher. *Die Rehobother Bastards und das Bastardierungsproblem beim Menschen,* 1913, 327 pp.

4. Pages 280 and 283. C. B. Davenport. *The Effects of Race Intermingling.* Proceedings of the American Philosophical Society, Vol. 56, 1917, pp. 364–368.

5. Pages 281 and 283. A. Lang. *Experimentelle Vererbungslehre.* Vol. 1, 1914, p. 727.

6. Pages 282 and 284. C. B. Davenport, and M. Steggerda. *Race Crossing in Jamaica.* Publication No. 395 of the Carnegie Institution of Washington, 1929, 516 pp.

7. Page 284. C. C. Brigham. *A Study of American Intelligence.* Princeton, 1923, 210 pp.

8. Page 286. C. B. Davenport. *Race Crossing in Jamaica. Scientific* Monthly, Vol. 28, 1928, 225–238. See also by the same author: *Do the Races Differ in Mental Capacity?* Human Biology, Vol. 1, 1929, pp. 70–89; and by W. E. Castle, *Biological and Social Consequences of Race Crossing.* American Journal of Physical Anthropology, Vol. 9, 1926, 145–156.

XIII

BIOLOGY AND SELVES

This chapter sets forth biological relations that appear of speculative interest in connection with existence of conscious selves; selves that may use the word "I." Such selves are among the most conspicuous phenomena of biology. Possibly they are its most characteristic and fundamental feature. The relations here presented do not lead to positive nor practical conclusions, but they illustrate the nature of biology.

To biological science, any species, any group of related organisms, presents itself as a series of successive and interwoven generations. Taken together, the generations constitute a great web or network. This network extends indefinitely forward and backward in time. It is formed by innumerable strands, the genes, which pass continuously through the net; which interweave, and at intervals are gathered into knots, that we call individuals. From the knots, the strands again issue, separate, interweave with other strands, and form new knots, individuals of a new generation.

Thus any individual—you or I—is a knot of strands, of genes, that extend backward into the remote past, there forming other individuals, and that will extend forward into the future, forming still others. Every knot, every individual, is a new combination of strands, diverse from the combination forming any other, but containing strands that have been part of many earlier individuals. The personal peculiarities of any individual, his characteristics, depend in large measure on what combination of strands has entered into him.

As material organisms potentially visible, you and I have been in existence ever since the race that developed into human beings began. This is literal truth. An unlimited microscopist could have followed with his eyes your course and my course down through countless ages, never losing sight of the material organisms for an instant; as the experimenter follows day by day his thousands of generations of infusoria. You and I were in material existence as living organisms, and indeed millions of years old, when the pyramids were built, and the unlimited microscopist could give our history from that time to this, without a break.

But as he followed us, we would not maintain our unity, our personal identity. Tracing the strands from you and from me backward in time, they diverge, into hundreds, into thousands of earlier individuals, with different characteristics. And if they are traced forward into the future, they again diverge, uniting with those from other individuals, to form a multitude of new personalities. The strands that make you have come from a hundred other individuals, and will later pass to other hundreds. Of your store of genes you may say, as Iago said of his purse, " 'Twas mine, 'tis his, and has been slave to thousands."

As a feeling, experiencing, knowing self, I, the ego, am identified with only one of the great number of knots into which the living strands are tied; my experiences cling to one of these exclusively. This fact arouses questions. Why should my experience not embrace the entire network, the entire organism, instead of merely one knot of its interlaced strands? What is the relation of my self to the other knots existing at the same time? And what is the relation of my self to the knots that came earlier and will follow later?

Playing a most important role for these questions is a further fact of biology. When the genes become knotted together to form an individual, the knot grows, develops, produces a fruit that hangs on the great netted vine. That fruit—the body of the individual—though all its parts can be traced back in unbroken genetic continuity to remote past ages, does not as a whole continue forward into the future. It carries within itself, besides the genes that have developed and transformed to produce the body, sets of genes that have remained in the unchanged, undeveloped condition. And it is these unchanged genes that continue into the future. The rest of the fruit drops from the vine and disappears.

The individual self appears, from straightforward biological observation, to be identified with the developed body, rather than with the undeveloped genes that it contains. Its experiences as a self seem to cease with the disappearance of that body, even though the genes that made it continue to exist and produce other bodies.

But the individual self has a singular wish to trace its existence forward into the future; the fact that it can be traced backward into the past is of less interest. Why should not the body that is produced anew by the genes which have given origin to that individual, constitute the same self as that individual—the same in the sense that my self now is the same as my self a year ago? There seems no inherent reason why this might not be the case. Many non-scientific theories of immortality have held that we do continue to exist as selves in later generations, although we do not remember our previous lives. This latter proviso is a relapse into science; for we each observe, upon inspection, that we do not remember a previous existence. But a perplexing situation would result if such theories were correct. The genes that constitute me do not, as they stand, produce directly another self. Before another self arises, half of my genes are lost, and the remaining half unites with half of the genes from another self. And so, if this theory were correct, the new individual would be the continuation, not of one previous self, but of two. And this recombination has happened thousands of times in the past. Each new individual that arises must then be the partial reincarnation of a thousand diverse individuals of the past.

And again, the genes from my self do not constitute merely one later individual. In different combinations they enter (in later generations) into many. Each of them must be a continuation of my self if any of them is.

But leaving aside these perplexing questions of many selves continuing into one and of one continuing into many, what difference would there be between, on the one hand, reincarnation without remembrance of previous experiences, and, on the other hand, the reliving of our characteristics in descendants, when our genes develop anew the character and traits that now exist in us? If *you* are a reincarnation of former individuals without remembrance, and *I* am a re-development of the characteristics of former individuals, there would appear to be no pragmatic difference between the two cases; no difference that could be detected by experience or experiment. The fact that we relive in posterity would seem to include all that would be included in reincarnation without remembrance.

And if this is the case, then all that it includes we already have. There exist even now many other individuals that bear in part the same genes as ourselves—in the same sense that posterity will bear them. That is, their genes and ours were derived by the division of the same pre-existing genes. The individual that leaves no children shares in this type of immortality with him that leaves offspring.

What is the relation of my self, identified as it is with one particular knot in the great network that constitutes humanity, to the other knots now existing? Why should I be identified with one only? To an observer standing apart from the net, it will not appear surprising that the different knots, since they are formed of diverse combinations of strands, should have different peculiarities, different characteristics. But that the observer himself—his total possibility of experience, that without which the universe for him would be non-existent—that he himself should be tied in relations of identity to a single one of the millions of knots in the net of strands that have come down from the unbeginning past—this to the observer appears astonishing, perplexing. Through the operation of what determining causes is my self, my entire possibility of experiencing the universe, bound to this particular one of the combination of strands, to the exclusion of some millions of others? Would *I* never have been, would *I* have lost my chance to participate in experience, would the universe never have existed for me, if this particular combination had not been made?

Certain facts of biology seem to bear on this question. My self has, as a matter of fact, arisen in connection with a particular union of two germ cells, each bearing a certain combination of genes. Could any other combination have produced me, produced my particular consciousness?

We find that other combinations are produced in great numbers, but that none of these do as a matter of fact produce my self, not even when they are combinations of germ cells from the same two parents. Suppose that my particular combination of germ cells had never been made, then seemingly those other combinations that *are* made would produce the same results that they now produce—namely, individuals that are *not* I. Then my personal possibility of existence would have been forever cut off.

If the existence of *me* is thus tied to the formation of a particular combination of genes, one may enter upon calculations as to the chances that I should ever have existed. What are the chances that the combination which produced me should ever have been made?

According to competent authorities, one of the two preexisting combinations from which my combination was derived, one of my parents, possessed somewhat more than 17,000 germ cells, while the other had the very considerable number of 300 billions. Every germ cell has a different combination of genes. And any one of the 300 billions from one parent might have united with any of the 17 thousand from the other. The chance that my particular combination of genes should have been formed was then about one in some five millions of billions.

But this gives only a minute fraction of the odds against my existence, or your existence, if each of us depends on the occurrence of some particular combination of genes. We have taken my two parents and their union as given. But the chances were equally many thousands of billions to one against the existence of each of them, and even existing, they might have mated otherwise, absolutely precluding the possibility of that combination of genes to which my consciousness is attached. And if we go back many generations, applying as we must the same considerations to each, we see that the system of notation which humanity has devised would be inadequate to express the odds against the formation of the gene combination from which I was derived, or you were derived. If we depend on the occurrence of the exact combination of genes that as a matter of fact produced us, the odds are practically infinite against your existence or my existence.

And what about the selves that would have come into existence if other combinations of genes had been made? If each diverse combination yields a different *self,* then there existed in the two parents the potentialities, the actual beginnings, of thousands of billions of selves, of personalities, as distinct as you and I. Each of these existed in a form as real as your existence and my existence before our component germ cells had united. Of these thousands of billions, but four or five come to fruition. What has become of the others? A thousand earths might have been populated with these personalities now consigned to the limbo of nothingness. Or if we include in our thoughts the combinations that might have been formed by union of other persons, and by previous generations, what must we conclude? An infinity of potential, inchoate, selves is cancelled in each generation, a potential and inchoate population sufficient to people all the regions that mythology has invented, all the worlds that astronomy has discovered. Our instincts and education impel us to regard a human personality as the highest and most real of entities, having attributes of worth possessed by nothing else. What are we to say of this infinite number of personalities whose existence was foreshadowed and prepared in exactly the way that gave origin to you and to me; who depended only on a chance meeting of particular germ cells for their full fruition, yet never advanced further? Nature, it appears, plays in the same infinitely wasteful way, whether with the spores of fungi and the eggs of fish, or with the potencies and beginnings of human personalities.

It is not strange that with the instincts and the education which they have, men should turn away from such a view of nature, and should attempt to find some alternative that does not lead to such conclusions. To persons that have from studies in philosophy or other fields reached the conviction that the self is the one certain reality, that relation to it is the touchstone of knowledge, and who from that conviction have drawn further conclusions—to such persons it may well seem that some other alternative must be found.

No alternative can be correct that is inconsistent with what occurs in biology. Can another point of view be found that is not incompatible with established biological science?

Possibly a basis for another point of view can be found through an attack on the assumption that it is diversity of gene combinations that gives origin to distinctness of selves. There are facts of biology that raise doubt as to this, that at least force upon us certain distinctions, certain qualifications of that assumption. A particular combination of genes does not always give rise to the same personal self, the same personal consciousness. A given gene combination, formed by union of two particular germ cells, sometimes produces one single self, sometimes two. It sometimes gives rise to two separate consciousnesses instead of to one. The very same gene combination that ordinarily produces one individual may be caused to produce two.[1] Then we have what are called identical twins. Their characteristics are similar, are objectively as nearly identical as two separate units can be. But they are distinct persons, distinct selves. They have distinct bodies, distinct sensations, distinct consciousnesses. If I am one member of a pair of identical twins, I do not feel pain when the other twin crushes his finger; I may not know that this has occurred. My twin may keep a secret from me; he may have thoughts that I have not, knowledge that I lack. His death is not my death. I and my twin are two separate selves, separate *I's*. How shall twin number one answer the question: How does it happen that my consciousness, my possibility of experience, is tied to this particular knot in the web, while there is another knot with the same constitution, the same genes, that is not-I?

And there are other facts of biology that raise similar difficulties. Two eggs that would separately develop into two distinct individuals, may be brought to unite, whereupon the two together produce but a single individual. This has been done experimentally in various lower organisms.[2] It has not been done experimentally in man, but that is merely from difficulties of technique. For the two selves of a pair of identical twins would certainly have been but one if the accident which caused two centers of development in the egg had not occurred. What is the relation of the self produced by the union of two originally diverse eggs, to the selves that would have come into being if the two eggs had remained separate? Is it identical with one rather than the other? Or with neither? Would *I* have existed, if the cell that produced me had united with a second cell which would otherwise have produced someone else? If so, then I would have existed with other characteristics than those which I have; for I should have had a set of genes diverse from those which I have.

To such questions biology has no answer. It has no answer to the general question: How does it happen that a particular self—my self—is tied to a particular combination of genes? It is not the nature of the combination that decides this; for the same combination of genes may exist, as we have seen, and yield an individual that is not-I.

From such facts it could perhaps be argued that the existence of my self is in some way one of the determining factors for what shall be produced by other germ cells, whether having the same combination of genes, or a different one. In that case, if I did not exist, some of the other germ cells might produce a different result from what they do produce; they might in that case produce *my* self. And so I would have existed, even though the particular union of germ cells that did in fact produce me had never occurred!

To work this out in detail, one would apparently have to hold that the human self is an entity existing independently of genes and gene combinations; and that it merely enters at times into relations with one of the knots formed by the living web. If one particular combination or knot should not occur, it would enter into another. Then each of us might have existed with quite different characteristics from those we have —as our characteristics would indeed be different if we had lived under different environments. The relation of the self to genes would be like its relation to environmental conditions; the particular combination of genes acting upon it would help to determine its characteristics; but would not determine its total existence as a self.

How simple and satisfactory this view would appear, as compared with the puzzle presented by strictly biological considerations! Neglecting all difficult details as to when and how the temporary union of the self and the body is made, it could be held that there is a limited store of selves ready to play their part, that the mere occurrence of two particular cells which may or may not unite has no determining value for the existence of these selves, but merely furnishes a substratum to which for reasons unknown they may become temporarily attached. And therefore there would be no cancellation of billions of inchoate human personalities, such as that to which the other view leads. And what interesting corollaries might be drawn from such a doctrine, as to the further independent existence of the selves after the dispersal of the gene combinations to which they had been attached!

Certainly no one can claim that biological science establishes or indeed favors that doctrine. But since biology itself furnishes no positive doctrine of the relation of selves to gene combinations, the question is a fair one: Does biological science make the holding of that doctrine impossible?

NOTES AND REFERENCES ON CHAPTER XIII

1. Page 296. See T. H. Morgan, *Two Embryos from one Egg.* Scientific Monthly, Vol. 18 (1924), pp. 529–546. Also H. H. Newman, *The Biology of Twins* (Chicago, 1917).

2. Page 297. See T. H. Morgan, *One Embryo from two Eggs.* Scientific Monthly, Vol. 18 (1924), pp. 354–371.

XIV

HOW THE INHERITED CONSTITUTION BECOMES CHANGED. THE ORIGIN OF DIVERSE ORGANIC TYPES

KNOWLEDGE of the production of new organic types has passed into a new phase as distinctly as has knowledge of heredity. No longer is this a subject for uncontrolled speculation; no longer is one man's opinion here as good as any other's. A great body of established facts is available in answer to the question: How are new organic types, having new hereditary characteristics, produced?

Dependence on Changes in the Genetic System

The genetic system, on which the characteristics of organisms depend, has become visible. Its operation, on which depend the methods of inheritance, has become open to inspection, as in a moving picture. By changes in this system the characteristics of the organisms are altered: new types are produced. By changes in its operation, new methods of inheritance are brought about. And such changes in the system, and in its operation, have been observed and are now under observation, in great numbers. The new types of organisms so produced exist and are multiplying, often giving origin again to other new types. Transformism in organisms is no longer a theory; it is an observed process, steadily in operation.

Knowledge thus far is mainly of small steps, as is bound to be the case at the beginning. Transformation of lower organisms into higher ones is not seen to occur in single steps; there is no reason to suppose that it does occur in single steps. Such small steps as are seen, when many times repeated, will result in great changes. How a complex organism is produced from a simple one—on this much remains dark; here there is still opportunity for speculative discussion. But the transformation of one type into another, the production of many types from one—of these things great numbers of instances are before us. And many of the processes underlying these transformations are displayed to view.

Since the characteristics of organisms depend on the genetic system—on the genes and chromosomes—it must be through changes in this system that new types will be produced. And observation and experiment have shown that this is indeed the case. The genetic system must be the point of attack for any agency that is to change organic types. Changes that do not affect the genetic system are lost; they do not reappear in descendants.

Two Types of Change: in Organization and in Materials

The genetic system becomes changed in two main ways, both giving rise to types with new characteristics. On the one hand its organization becomes changed. The substances which make up the genetic system—the genes—are not scattered and separate. On the contrary, they are organized into a somewhat elaborate machinery, the chromosomal apparatus. This apparatus undergoes a series of complex operations, by means of which the genes are distributed to the germ cells that are produced; and the individuals of the next generation each receive a complete copy of the existing apparatus.

When the operations of this elaborate apparatus were studied, the first impression was one of the regularity and precision of its performance; of the accuracy with which the offspring receive an exact copy of the whole. But minute study of great numbers of different individuals later revealed that inaccuracies and aberrations at times occur. In many different ways the machinery is found sometimes to diverge from the stereotyped plan of operation. Then its products are not alike. Unusual combinations of materials pass into some of the new individuals, and they show in consequence a new set of characteristics. The new combination of materials now works in a different manner, so that a new scheme of inheritance is revealed. The new types produced perpetuate themselves, with new rules of inheritance. Great numbers of such changes occur, as we shall see when we take up details. The genetic system, though it remains constant in its operation for long periods, reveals itself finally as not fixed and stereotyped, but mutable, producing new things. And of late means have been found for intervening in its operations. Radiations have been found to affect it, so that some or all of the changes that occur in nature can be produced, and their results bred and multiplied.

The second type of change observed in the genetic system consists of alterations in the nature of the materials that compose it; consists in changes in the genes themselves. These materials at first seemed unchanging and permanent, just as did the organization of the system. But now that methods of testing the nature of the genes have come to general knowledge, and thousands of skilled observers are concentrating their attention on them, in many diverse organisms, these materials too are found at times to become altered in nature. In a thousand cases observed, mayhap no changes will be found. But when the number of cases examined rises into the tens of thousands, into the hundreds of thousands (as is now the situation), instances of changes in the genes are found; changes giving origin to altered characteristics. And these changed genes increase and multiply, as they did before alteration, so that entire populations can be produced, are produced, with the consequent changed characteristics. So arise new types. Great numbers of diverse changes in the genes—the so-called gene mutations—have now been observed and the new types perpetuated. And here too, in the action of radiations has been found a method by which changes in the material of the genes may be produced, so that new types result and can be propagated.

By the processes of biparental reproduction the results of both of the types of change—alteration in the organization of the genetic system, alteration in the unit materials of which it is made—can be combined in many ways, giving rise to so vast an array of changed types as can hardly be conceived or surveyed. The results of these processes are at the present time merely coming into view. Their ultimate potentialities, the limits of their consequences, no one can as yet expound.

Consequent Appearance of New Types

In these two ways then vast numbers of new types are appearing. Some of these form efficient physiological machines, others do not. Some of them yield individuals that are fitted to survive under the conditions in which they occur; others, individuals not fitted to survive. A great number of the new combinations formed therefore disappear, sooner or later; only a remnant is saved. Selective elimination occurs on a vast scale, a scale hitherto unsuspected. It is one of the chief features in the observed process of transformation of organic types. Production of new types of organization in the genetic system; alteration of the genes themselves; consequent change of characteristics; propagation and multiplication of the changed types; and selective elimination on a great scale, as time passes—these are the features of the process, all of which are observable, and have been observed in many examples.

With this preliminary sketch of the main features in the production of new types, let us turn to some details and examples of each of these features.

Changes in the Organization of the Genetic System

Simplest of the alterations in the organization of the genetic system are perhaps the changes in the number of chromosomes present, with the attendant changes in the number of representatives of each kind of gene.[1] The most common situation, as we have seen in earlier chapters, is that each individual has its chromosomes in pairs, one member of each pair from each parent. Two representatives of each chromosome are therefore present, so that the individual may be said to have two complete sets of chromosomes. Consequently it has two representatives of each kind of gene; two complete sets of genes. This condition is maintained in succeeding generations through the fact that each germ cell receives only one set of chromosomes, one set of genes. By the union of two such germ cells, the condition with two sets is restored. This is the situation in human beings and in most other organisms.

Change in Number of Sets of Chromosomes

But the number of sets of chromosomes and of genes may become altered, in various ways. Sometimes a single germ cell retains all the chromosomes—two sets instead of the usual one. This can be brought about in some cases by subjecting the dividing cells to low temperature. In this way a division of the cell body is suppressed, so that a single germ cell retains all the chromosomes that should have been distributed to two. When one of these germ cells with two sets of chromosomes unites with the usual type, having but one set, an individual is produced having three sets of chromosomes, three representatives of each kind of gene, instead of two. Or if two of the germ cells each bearing two sets unite, there is produced an individual with four sets of chromosomes—four representatives of each type of chromosome, and of each type of gene. (See the diagrams of figure 50.)

Such individuals with three or four sets of chromosomes or genes, in place of two, are now known for many organisms. They differ in many respects from the individuals having but two sets. Those having three sets are known as triploids. These reproduce in an irregular way, because of course the three chromosomes of each type cannot pair in the usual way, one passing to each of two germ cells. Some of the germ cells receive one representative of some of the chromosomes, two of others. The consequence is that most of the germ cells, having irregular numbers of chromosomes, are not functional;

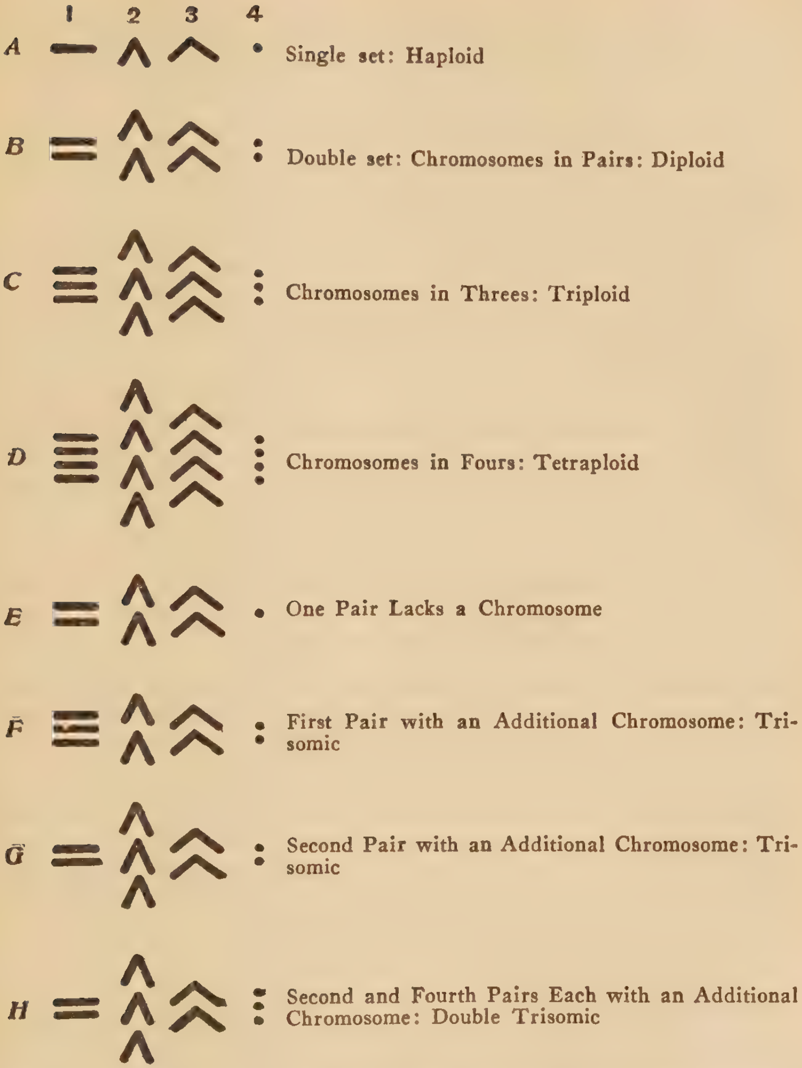

1
2
3
4
A
Single set: Haploid
B
Double set: Chromosomes in Pairs: Diploid
C
Chromosomes in Threes: Triploid
D
Chromosomes in Fours: Tetraploid
E
One Pair Lacks a Chromosome
F
First Pair with an Additional Chromosome: Trisomic
G
Second Pair with an Additional Chromosome: Trisomic
H
Second and Fourth Pairs Each with an Additional Chromosome: Double Trisomic

Figure 50—Diagrams to show the different groups of chromosomes that produce diverse types of organisms. As a basis for the diagram the single set of four chromosomes of Drosophila melanogaster is taken; such a single set is shown at A. A to H, the chromosomal groups in certain known types of organisms. B, the diploid condition, is that found in most animals and plants.

they give rise to no individuals. A few of the germ cells receiving either one complete set, or two complete sets, are functional. They produce in the next generation, therefore, a few offspring like themselves with three sets of chromosomes, and a few of the usual type, with two sets of chromosomes. But in plants, such triploid individuals can be propagated by bulbs, cuttings and the like, so that they form permanent varieties. Such varieties are common in the ornamental plants that are so propagated; in tulips, hyacinths, dahlias and the like. They aid greatly in producing the great numbers of diverse forms, colors and sizes, in such plants.

Individuals with four sets of chromosomes and genes (known as tetraploids) may be nearly or quite stable, reproducing themselves as do those with but two sets, though some of them are unstable, like the triploids. They differ in their characteristics from the usual individuals. They are larger, with thicker stems, larger flowers, leaves, and other organs, diverse methods of branching, and the like. One of the first of the mutations of the evening primrose cultivated by de Vries was of this nature. From its greater size it was given the name Oenothera gigas, the giant evening primrose. Later it was discovered that it owes its peculiarities to having four sets of chromosomes—28 in all (in place of the usual 14, forming two sets). It turns out that a considerable number of the "mutations" observed in plants are of this sort. Giant forms resulting from the same peculiarity of the chromosomes have since been found in many plants, and in some animals. They are among the commonest varieties in the ornamental plants that vary so much in size, color and form, giving rise particularly to the very large varieties.[2]

Many wild plants show some species that have two sets of chromosomes, others that have three, others that have four. The number of sets may be still greater, up to eight or ten or more. It appears clear that a change in the number of sets of chromosomes has been an important factor in the origin of diverse species, in such groups. In the wild roses, the number of chromosomes in a single set—that is, the number of originally diverse kinds of chromosomes—is seven. Some of the species have 14 chromosomes, or two sets; others 21, others 28, 35, 42, 56. That is, different species have respectively 2, 3, 4, 5, 6, or 8 sets of chromosomes, each set containing 7. In the chrysanthemums, where the number in a set is nine, there are species with respectively 18, 36, 54, 72 and 90 chromosomes; that is with 2, 4, 6, 8, and 10 sets, respectively. In the bananas, having 8 chromosomes to a set, there are different species with respectively 16, 24, 32, and 48 chromosomes. Similar differences are found among the different types of wheat, of strawberries, and of many other plants. Changes in number of sets of chromosomes plays a large role in the origin of varieties and species.

A fact of great interest is that these varieties with increased numbers of chromosomes show a marked tendency to reproduce without fertilization.[3] This does not happen in all such varieties, but it does in many of them. In such cases the female germ cell or ovule does not reduce its number of chromosomes, but retains them all, and develops a plant without union with a male germ cell. It is as if an increased number of chromosomes tends to cause the egg cell to develop, whether the increase is brought about by fertilization or in some other way. This power of producing new individuals from seeds that are not fertilized is of great importance for these varieties with numerous sets of chromosomes. For when many sets are present, the processes of pairing and reducing the number of chromosomes occur irregularly, so that many or most of the germ cells produced are not functional. By omitting the pairing, reduction, and fertilization, the variety is enabled to propagate and multiply, remaining true to type.

Addition or Subtraction of One or Two Chromosomes

Another set of varieties is produced by adding or subtracting, not an entire set of chromosomes, but only one single chromosome. This increases or decreases by one the number present of some single one of the kinds of chromosomes existing in the organism. Typically, as we know, there are present in the individual two chromosomes of each kind, the chromosomes being in pairs. By some of the irregular divisions that occur at times, one of the kinds of chromosomes may have its number reduced to one, or increased to three. (See the diagrams, figure 50.) This causes a change in the characteristics of the individuals that develop, so giving rise to a new type or variety, which may be propagated and multiplied.

If any one of the usual kinds of chromosomes is completely lacking, this as a rule entirely prevents development, so that no varieties of this kind occur. If a chromosome has present but one representative in place of the usual two, this has different effects, depending on what chromosome it is that is lacking. If it is one of the large chromosomes, bearing many genes, usually development will not occur, even though there remains a single one of the chromosomes of that type. If it is a smaller and less inclusive chromosome that is lacking, the result is to change the characteristics of the individuals produced. In the ordinary reproduction of many organisms, as is well known, a very great change in the individuals is made, depending on whether two X-chromosomes are present, or only one. If two are present the individual becomes a female, if but one, a male (this is so in most insects and in mammals, as well as many other groups). When it is not the X-chromosome, but some other that is single, other changes in characteristics result.

Most common perhaps are the changes that result from adding one representative to some single pair of chromosomes, so that there are three chromosomes present of that kind, though only two of the other kinds. Such changes have been extensively studied in the common Jimson weed, Datura stramonium, by Blakeslee and Belling and their associates.[4] The Jimson weed has 12 chromosomes to a complete set; so that the usual plants, with two sets, have 24 chromosomes. By adding one chromosome to one of these 12 pairs, individuals with 25 chromosomes are produced. Since any one of the 12 different chromosomes may thus have an additional representative, 12 different types of plants are thus producible. Eleven of these possible twelve have been produced and recognized. Each differs in many features from the usual plants having but two chromosomes to each pair; and each one differs from every other that is produced by adding one chromosome to some other one of the 12 chromosome pairs. The differences are not slight but marked and striking. There are such differences in the form, size, and vigor of the plants, in the shape and size of the leaves, in the method of branching, in the form, size and structure of the fruit, and in the internal structure of the plant.

These eleven new types of Datura, each having twenty-five chromosomes, show peculiar features of inheritance. In producing their germ cells, half of the germ cells receive twelve chromosomes, the other half of them thirteen chromosomes. By union of two germ cells with twelve chromosomes each, offspring are produced with the original number of twenty-four chromosomes. These offspring are therefore of the usual typical structure; they have "reverted to type," and are not like their aberrant parents. By the union of the germ cell having 12 chromosomes with another containing 13, offspring are produced that are again like the aberrant parent, having 25 chromosomes. When two germ cells containing each 13 chromosomes unite, usually the offspring do not develop. In rare instances they do. They then form a new type of individual, with 26 chromosomes, there being 4 representatives of one kind of chromosome, two of each of the others. On the whole therefore these various types with 25 chromosomes reproduce themselves, in seed reproduction, in only a part of their offspring, the rest going back to the usual type, or rarely producing still another type.

These plants with an additional chromosome show changed rules of inheritance in still another respect. One of their "pairs" of chromosomes has three chromosomes of a kind in place of two. If one of these chromosomes has a dominant gene A, the other two the corresponding recessive gene a, then if two such individuals are mated, the proportions of dominant and recessive individuals among the offspring is very different from that found in ordinary Mendelian inheritance. In Mendelian inheritance, where there are but two chromosomes of a kind, the proportion is three dominants to one recessive. In such a case as is mentioned above, the proportion is five dominants to four recessives, for the offspring having twenty-four chromosomes; seven dominants to two recessives for the offspring having twenty-five chromosomes. Still different ratios result if in place of three chromosomes of a kind there are four. The usual Mendelian ratios are characteristic of inheritance when there are two chromosomes of a kind; other numbers give other ratios.

If several of the chromosome pairs each have an additional chromosome, usually the individual will not develop. An "unbalanced" condition is produced that is fatal. But in the Jimson weed two pairs may have an additional member, and the individual will still develop. From 12 different chromosomes, 66 different combinations of two additional members can be produced. Of these 66 possible diverse types with 26 chromosomes, about 40 have been produced and observed by Blakeslee and his associates.

Plants will also live in which a single kind of chromosome has four representatives instead of two. There are 12 possible types of this kind in the Jimson weed; only one of them has been studied.

In this plant there are also types of the kind mentioned on previous pages, resulting from changes in the number of complete sets of chromosomes. There is a type having but a single set (12 chromosomes), others with 2, 3, and 4 sets. Additional still different types are producible by increasing or decreasing by one or two the number of representatives of some particular one of the 12 kinds of chromosomes, in individuals with 3 or 4 sets. A number of these have been observed.

Of these many possible types, resulting from the altering of the numbers present of particular chromosomes, or of changing the numbers of sets present, some 77 have been observed by the investigators at work on the Jimson weed. It can be computed that the total possible number, of the kinds of such types that can live and develop, is 3400. That is, of the ordinary Jimson weed, having just 12 different sorts of chromosomes, 3400 genetically diverse types may exist, resulting from mere shifting in the numbers and relative proportions of the different sorts of chromosomes present; with no change in any of the materials—the genes—of which the chromosomes are composed. Most or all of these types would reproduce themselves by seed in a certain proportion of their offspring, while reverting to the original type, or giving rise to others types, in the rest.

There is no reason to suppose that the Jimson weed is unique in these respects. Other plants are known that show the same phenomena. In the evening primroses, Oenothera, there are similarly great numbers of different types, many of which are known to be produced in the same way as in the Jimson weed.[5] There are types with two sets of chromosomes, with three, and with four. And there are many diverse types produced by adding a single chromosome to the sets, or subtracting one. Many or most of the mutations of Oenothera, described by de Vries and others, turn out to have been produced in these ways. Similar phenomena are being discovered in many other plants, though no others thus far have been so fully studied as the Jimson weed and the evening primrose.

In any plants that can reproduce by bulbs, cuttings, runners, or the like, or that can reproduce from unfertilized seed, these numerous types produced by altering the number and balance of the chromosomes can propagate and multiply indefinitely. Many of the extremely numerous varieties of ornamental flowering plants, such as we find in tulips, roses, dahlias, chrysanthemums, hyacinths, and the like, beyond doubt have their origin in these changes in the number and balance of the chromosomes. Such changes account for a large share of the manifoldness of type found in living things.

Change in Structure of Particular Chromosomes

Still another large group of types owe their origin to changes in the structure of individual chromosomes. The single chromosome, as we have before seen, is a segment of the chain of genes, each gene having its definite place in the chain. By the action of radiations, and in other ways unknown, the chromosomes at times become broken into pieces.[6] A piece of one chromosome may come in contact with another, and stick to it. One of the chromosomes thus loses a part of its genes, while another gains additional genes. Thus are produced chromosomes that are deficient with respect to certain genes; and others that are double for a certain number of their genes. These changes cause alteration in the method of operation of the genetic system. In consequence the methods of inheritance are changed. In some cases the change in the chromosomes can be seen by examination under the microscope, while the corresponding change in reproduction and inheritance is discovered by breeding individuals having the changed chromosomes. A considerable number of cases studied in both ways have been described and figured by Painter and Muller.[7]

In the majority of cases, perhaps, such changes in the chromosomes do not give rise to new types that can multiply; rather do they give rise to irregularities that in the long run result in the destruction of the organisms bearing the changed chromosomes. But there are numbers of new and lasting types that have been formed in this manner. In the Jimson weed, in addition to the many classes of types resulting from changes in the numbers of chromosomes (already described), there are large numbers of other types that result from alterations in the structure of the chromosomes. A single chromosome loses one of its halves, while its other half is doubled. Thus, if the normal chromosome is composed of the chain of successive genes a-b-c-d-e-f-g-h, such an altered chromosome has the genes a-b-c-d-d-c-b-a. In the pairing of the chromosomes at germ-cell formation, there is opportunity for such a change to occur. Blakeslee and his associates have found many types in the Jimson weed in which this has occurred in one chromosome or another of the twelve kinds. Such types are diverse from those described on previous pages. In still other cases, parts of separate chromosomes have become united, giving rise to still other types. The number of diverse types, capable of life and development, that are to be expected in consequence of mere changes in the numbers of chromosomes is about 3400, as we have before set forth. When to these are added the diverse types that result from shifting about and recombining parts of single chromosomes, the number of such diverse types possible is increased to above 10,000. All these are derivable by altering the way in which the 12 different chromosomes are combined, without change in the nature of the materials of which the chromosomes are composed.

This situation is probably typical for plants. A great proportion of the variety of organic forms and structures there found are due to these processes of altering the numbers and combinations of the chromosomes, and of their component parts.

In higher animals some of these methods of altering the organization of the genetic system are less effective in producing lasting diversity of type. This is because higher animals have no methods of multiplying from a single parent, comparable to the propagation of plants by bulbs, tubers, cuttings, and the like. Hence in animals, while changes in the relative numbers and structure of the chromosomes probably occur as frequently as they do in plants, they often result in irregular formation of germ cells, and consequent failure of the new types to propagate. Yet some of the new conditions produce new types that can be propagated. Such a new type, having strikingly different rules of inheritance from the usual type, has been produced under observation in the fruit-fly, Drosophila, and studied by L. V. Morgan,[8] and others. The two rod-shaped X-chromosomes of the female, that are ordinarily quite separate, have become in this type united at the tips into a V. Such individuals have been propagated and multiplied.

On account of the new type of inheritance that these animals show, they are extremely useful for the study of certain problems, and are much bred by investigators.

There are many indications that changes in the number and combinations of the chromosomes have played, in animals as well as plants, an important role in the formation of different natural species. Closely related species exist, one with two sets of chromosomes, another with four or more sets. In other cases, apparently two chromosomes that are separate in one species are united end to end to form a single chromosome, in another species. A most interesting set of examples of this sort of thing is found in different species of the fruit-flies, Drosophila (figure 51). Some of the species have four pairs of chromosomes, two of the component chromosomes being V-shaped, with a constriction at the point of the V, as if two chromosomes were here joined. Others have in place of one of these V's two straight chromosomes, such as would be formed by separating the halves of the V at the point. In still others, each of the two V's is replaced by two straight chromosomes. These relations are shown in figure 51. It appears highly probable that one of the factors in the change of species was the union of two straight chromosomes to form a V, or the reverse separation of the V into two straight chromosomes.[9]

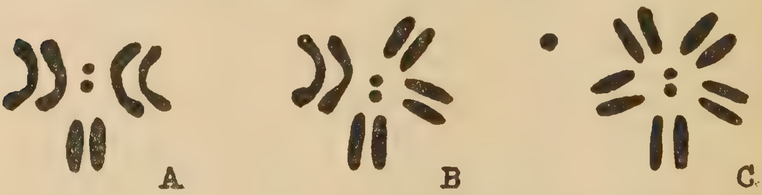


Figure 51—Chromosomes of three different species of Drosophila, having 8, 10, and 12 chromosomes respectively. A, Drosophila melanogaster; two V-shaped pairs. B, Drosophila obscura; the place of one of the V-shaped pairs is taken by two pairs of straight chromosomes, at the right. C, Drosophila virilis; the place of each of the two V-shaped pairs is taken by two pairs of straight chromosomes. After Metz, Moses and Mason (1923).

Great Number of New Types So Produced

All in all, it is clear that the number of diverse types of organisms in nature—whether we call them breeds, races, varieties, species, or what not—is immensely increased by alterations which occur in the organization of the genetic system; in the way the genes and chromosomes are combined. The occurrence of such alterations, giving rise to new types, has been many times observed. And the conditions found in many of the diverse types existing in domestication and in nature are such as would be produced by alterations of this kind.

Changes in the Material of the Genetic System: Gene Mutation

To the great number of types produced by these alterations in the organization of the genetic system must be added another great multitude resulting from alterations of the nature of the materials of which the genetic system is composed: alterations of the genes themselves. These changes, commonly spoken of as gene *mutations,* are perhaps more fundamental, more far-reaching in their results, than those due to the changes in organization.

As we have seen in earlier chapters, there are methods by which the location of particular genes in the chromosomes can be discovered. In these ways a particular gene can be identified, and its nature and effects in different individuals determined. When many individuals, descended from the same parents, are thus examined, it is found that in some of them a particular known gene has become changed in its nature. In these it produces effects on the characteristics that are different from its effects in the other individuals. A certain gene in the fruit-fly causes the eye to be red. It becomes so changed in some individuals as to cause the eye to be white. This is a typical example of a gene mutation.

Cause of Gene Mutation

When a very large number of individuals are bred, such mutations are found to occur in a few of them, the cause of the mutations not being apparent. Study has shown that the mutation affects only one of the two like genes of the pairs of genes that are present in the cell. Hence the change is not due to some general condition of the body, or even of the entire cell, but to some agent whose action is so minutely localized that it affects only one of two like genes in the same cell. Of late an agency acting on genes in this minutely defined way has been discovered; such mutations can be induced by radiations, particularly X-rays. When the developing organism is subjected to the rays, these act directly on some of the genes, altering them but not destroying them. The altered genes continue to live and multiply in the altered condition, as the cells divide; and to influence the characteristics of the organism, giving rise to new characteristics. The recent discovery of this method of altering genes, by H. J. Muller,[10] is one of the epoch-making discoveries of biology. But even when a large number of individuals are subjected to the radiations, in only a few are any genes so altered as to yield mutations.

What is the cause of the occurrence of gene mutations, in individuals that are not subjected to X-rays? It has been suggested that the rays of short wave-length coming from radioactive substances of the earth's crust or from the depths of space may be the agency that produces mutations. If this is so, the genes of all organisms are undergoing a continuous bombardment by which they are altered. This matter is further discussed in the next chapter.

Same Gene Changeable in Different Ways

It has been found that the same gene may, in different individuals, become changed in many different ways. The same gene that when altered in a certain way causes the usually red eye of the fruit-fly to be white, becomes changed in other individuals so as to give a pinkish color ("eosin"). In still others it is so changed as to give a buff color. This particular gene has been found indeed to become, in different individuals, changed in at least eleven different ways—each of these yielding a different type of eye color. Each of the types of individuals so produced can be bred and multiplied, along with the original red-eyed individuals. Thus from the red-eyed type have been produced in the course of twenty years eleven different types; all from different modifications of the same gene, and all of them lasting types, transmitting their peculiarities (by way of these genes) to their descendants.[11] The single gene has many possibilities of transformation.

Diverse Characteristics Produced

Seemingly any of the organism's genes may thus become changed, in one or more ways. Several hundred diverse genes have thus become changed in the fruit-fly Drosophila, while it has been under observation in the last twenty years. These changes affect every possible inherited characteristic: size, form, and function of the wings; structure and number of legs; color of the body; size, form, number, and distribution of the bristles on the body; structure, size, color, and function of the eyes; the senses of the animal, its health, vigor, and power of reproduction. An indefinitely great number of diverse types have thus been produced from this single species, these types differing in single characteristics of the kinds mentioned above, or in combinations of characteristics. Each type is as permanent as the original one, so far as the inheritance of its characteristic features is concerned. Almost all the diverse hereditary characteristics whose inheritance has been described in our earlier chapters have arisen through such gene mutations.[12]

The gene mutations may result in either intensifying or weakening certain characteristics, or in changing their nature or quality. Pigments may be intensified or diluted, or changed in color. Organs may be increased or decreased in number, or in size; they may be changed in distribution, or completely suppressed. Flies are thus produced having more than six legs; flies with smaller eyes or no eyes; flies with wings of changed form, smaller size, or with no wings; flies with bristles more or less numerous, of different forms and structure, and different distribution on the body; flies with eyes of all colors—white, buff, pink of many shades, purple, red of many shades and intensities. The change produced by mutation of a single gene may be extremely slight, or it may be very great. Naturally the first mutations discovered were those that produce a conspicuous effect, so that the impression arose that all mutations are of this character; a mutation was conceived to be a "large step," a "saltation" or leap from one condition to a very different one. But as observers have become more skilled in detecting mutations, it is found that the number which give origin to very slight changes in the organism is much greater than that of those that produce large changes in characteristics. Many gene mutations are now known that produce mere slight internal changes in the physiology of the organism, not detectable save by certain special tests. It is extremely probable that the number of such nearly imperceptible mutations greatly exceeds the number of those having conspicuous effects.

In other animals and plants that have been extensively studied, gene mutations occur as they do in the fruit-fly, affecting every characteristic. They have been much studied in pigeons, in fowls, in rats, mice, guinea pigs, and rabbits. In these animals they give rise to the very numerous domesticated varieties, differing in colors, patterns, and other features of their plumage, or coats; and in size, form, and structure. In cultivated plants they are likewise numerous, giving rise to diversities of color, form, size, and structure. Here their effects are usually combined with those resulting from changes in the numbers of chromosomes and from other alterations in the organization of the genetic system (described in the earlier part of this chapter). Thus results the inextricable tangle of varieties, races and types found in the cultivated plants.

Most Mutated Genes Recessive

Most of the mutated genes give characteristics that are recessive, as compared to the condition found in the unmutated individuals. That is, if a mutated gene and an unmutated gene are present in the same pair, the characteristic manifested in the individual is usually due to the unmutated gene. There are however a large number of mutated genes that are dominant; they manifest their effects even in the presence of the unmutated gene in the same pair.

Where Mutations Occur

In order to produce an individual with new characteristics that shall be inherited, a gene mutation must occur in a germ cell, or in some cell that is later to give origin to germ cells. These germ cells will then yield individuals having mutated genes in all their cells. Gene mutations may be produced in the ordinary cells of the body, that do not form germ cells; this has recently been demonstrated by the use of X-rays (Patterson[13]). This causes changes in some part of the body of the individual, but the offspring do not inherit these changes, for the body cells bearing the mutated gene do not transform into new individuals. It is clear, therefore, that not all mutations produce inherited changes in characteristics.

Frequency of Gene Mutations

How frequently do gene mutations occur? It is extremely difficult to obtain reliable statistics on this question. Muller and Altenburg[14] studied the frequency of a certain type of mutation—those preventing development—in the fruit-fly. They conclude that about one out of every thirteen individuals (in the case of females) undergo such a mutation in some gene. This conclusion cannot be transferred to other types of mutations, but it is clear that gene mutations are not extremely rare. During the twenty years in which the fruit-fly has been under careful observation by many workers, hundreds of diverse gene mutations have occurred. The rate of mutation is very greatly increased by subjection to X-rays. In one set of experiments, Muller reports that the rate was increased about 150 times by the X-rays.[15]

On the whole it is clear that gene mutations, altering the hereditary characteristics, are much more frequent than had been supposed. The twenty years in which hundreds of diverse gene mutations have appeared in the fruit-fly is an extremely short time in comparison with the length of geological epochs. Considered with relation to such epochs, there is a very rapid rate of change. As a result of these gene mutations, even though a race of organisms were at a given time "pure," in the sense that all its individuals had like genes, and so had like inherited characteristics, in a short time it would become "impure." That is, the genes of different individuals will have become diverse, giving breeds with different inherited characters. Such heterogeneity of inherited characteristics as we find in a population of any species, including man, arises therefore even without crossing of diverse races, within the limits of an originally homogeneous race. It is of course further greatly increased by crossing, both among the diverse breeds formed by mutations, and among the members of groups or races that have long been diverse.

Great Role of Selective Elimination

The gross and conspicuous consequences of the frequent mutations that occur are very largely determined by the fact that selective elimination occurs on a large scale. That is, some of the gene mutations yield individuals that are at a disadvantage; they are less efficient machines than others, or they are not fitted to the conditions in which they find themselves. Such individuals die without propagation; or they and their descendants are at a disadvantage, and gradually decrease and disappear. Observation indicates that in the various species of the fruit-flies, Drosophila, mutations occur among the individuals living in nature, as they do among those in the laboratory. But in nature, almost all the mutated individuals disappear. They are not so well fitted to the conditions of wild life as are those that have not mutated. In the laboratory these same mutated individuals can be given specially favorable conditions, so that they live and multiply. Thus in the laboratory the species becomes rapidly broken up into many diverse breeds, differing very greatly in their inherited characteristics; while in nature the species remains nearly uniform. There appears to be no indication that the wild population of the fruit-fly has changed in any appreciable way during the twenty years in which hundreds of mutations have appeared. In the wild population all the mutated breeds have disappeared.

A similar situation is found whenever a domesticated organism is compared with its congeners. There is reason to believe that mutations occur with equal frequency in both. But under the easier conditions of domestication, the mutated breeds can live and propagate, while under the conditions of wild life most of them disappear. Hence the domesticated population becomes differentiated into many breeds and varieties, while the wild population remains nearly uniform.

Disadvantageous Effects of Mutations

It is obvious that the disadvantageous effects of mutated genes are of great importance, and must be given serious consideration in judging the relation of these things to such transformations of organisms as have occurred during past geological ages, in judging their relation to progressive evolution. A large proportion of the gene mutations that produce conspicuous effects on the external characteristics of the organism are disadvantageous in their action. Wings or eyes are produced, in the fruit-fly, that do not function so well as do the unchanged organs. Deformities of all sorts are common results of mutations. Most of the conspicuous mutations result also in directly reducing the vigor and resistance of the organisms, and in shortening their lives. There are all grades of such effects. Many gene mutations are known that quite prevent the development of the animal, unless the mutated gene is accompanied in the same pair by one not mutated. Even though a normal gene is present, mutated genes of this sort frequently greatly reduce the vigor of the individuals, and some of them cause structural deformities. Other gene mutations permit the individual to develop, even though unaccompanied by an unmutated gene in the same pair, but decrease its vigor—in many different grades, in different cases. Some even of the conspicuous gene mutations affect the general vigor and resistance very little; perhaps not at all. Whether the very numerous inconspicuous mutations, having slight internal effects, are commonly disadvantageous in their action is not known; on the whole there is little evidence that they are.

These effects of conspicuous gene mutations on general vigor have been more fully observed in the fruit-fly than in other organisms. But there are many cases of the same sort known in others; and there are other indications that most of the conspicuous gene mutations are disadvantageous wherever present.

Relation to Progressive Evolution

What bearing has all this on the method of progressive evolution? It appears clear that organisms, as ages pass, in some way transform from simple to complex. This is shown by study of past geological epochs. Is gene mutation the method by which this has occurred (along perhaps with such changes in the organization of the genetic system as are discussed on earlier pages of this chapter)? When we see gene mutations in experimental breeding, have we before our eyes the process that has resulted in progressive evolution?

If all such mutations are destructive or disadvantageous, they cannot be the material of progressive evolution. Some investigators have therefore expressed the opinion that in gene mutations we are witnessing merely the disintegration of the genetic system, the breaking down of organisms, not their upbuilding; we are observing the "wrecking of the train," not its construction. The method of progressive evolution would then be still completely hidden from us.

To this it is answered that it is not known that all gene mutations are disadvantageous. For many of the mutations producing very slight changes, there is no indication of harmful effects. There are even certain conspicuous alterations which, it is practically certain, are not disadvantageous. Different colors in rabbits and rats arise by mutation; there appears to be no evidence that they result in decreased vigor. The diverse eye colors in man must originally have arisen by mutations: presumably blue eyes (since they are recessive) from darker eyes. Yet there is no indication that differences in vigor go with diverse eye colors.

It was to be anticipated that most changes in the materials of the genetic system, so drastic as to cause a sudden large alteration in the structure or physiology of the organism, would be harmful. But the case is different with respect to the much more numerous mutations causing very slight effects. Many of these too may be harmful, but some of them may not. Some of them may well make the individual more efficient under the conditions in which it lives. Even if but a small proportion of them are thus advantageous, this is sufficient. Individuals with these rare beneficial mutations will multiply, gradually supplanting those without the mutations. After a time a large proportion of the stock will consist of the individuals bearing the advantageously modified genes.[16]

Moreover, knowledge of the way the characteristics of organisms are determined shows that changes of inherited characteristics must have their origin in changes in the genes. But these are exactly gene mutations. If we saw the changes that result in progressive evolution, we should see changes in the nature of the genes and in the organization of the genetic system; and these are what we do see. The argument that they are not material for progressive evolution is self-destructive.

What appears to confuse the matter is that selective elimination plays a much greater role in the process than some have anticipated. By changes in the organization and materials of the genetic system, immense numbers of different types of organisms are produced. The very large majority of these are eliminated as a result of their lack of efficiency under the conditions. The populations that remain are a small remnant out of a great multitude that have perished. These are statements of observed facts. The remnant that survives then forms the basis for renewed mutations; renewed changes in the organization and material of the genetic system. Again the efficient combinations survive, while the great majority of imperfect and inefficient combinations disappear. And so the process continues for ages, in every period there being formed a great number of new types to undergo selective elimination.

Is Man Undergoing Mutation?

Is man undergoing this process? Are gene mutations occurring in man, as they are in the fruit-fly, the fowl, the rat, the guinea pig?

There is no reason for doubting that gene mutations occur in man as they do in other organisms. He has the same type of genetic system, composed of genes acting in the same manner. Owing to the length of a generation in man, changes resulting from mutations will require much more time, absolutely considered, than in such an organism as the fruit-fly, with a new generation every two or three weeks. But in the long run the result must be similar in the two cases. A race of men will in the course of time become heterogeneous, through the occurrence of mutations, quite without mixture with another race, just as occurs in plants and animals. Doubtless much of the variety in a human population is due to this cause.

The fact that most gene mutations are harmful appears disconcerting when applied to man. Civilized men live under conditions much resembling the domesticated conditions in which even harmfully mutated breeds of animals survive and propagate. If we conceive, as some have suggested, that gene mutations are the result of bombardment by short-wave radiations, there is something terrifying in the thought that we are continually under this bombardment, and that it injures the genes, which are the very foundations of personality. And the effect is the same whether due to such bombardment or to other causes. The genes are changing, and most of the changes, if we may judge from other organisms, appear to be for the worse. One might judge in haste that this means the necessary gradual deterioration of mankind. But it is certain that under these same conditions man has developed from organisms that, if we go back far enough, were inferior to him in structure and function; from organisms, even the more recent ones, that lacked many of his capabilities; that lacked particularly his powers of adjustment to conditions met. The situation therefore does not preclude further development in that direction. But it seems to imply the necessity, if there is to be advance, or even if there is not to be retrogression, of selective elimination on a vaster scale than is agreeable to contemplate in connection with man. Much of that selective elimination is bound to occur, and doubtless does now occur, in the germ cells themselves, and in the early stages of development, as happens in other organisms. The burning question is: How much of this elimination ought to be brought about after birth? This is essentially the subject dealt with in our Chapter X.

Summary

What is the general impression from a survey of the changes in the genetic system, and the consequent changes in hereditary characteristics observed during the last thirty years?

Such a survey shows that changes in genes, and in the organization of the genetic system, are occurring rather rapidly, when considered in connection with such long periods as must be held in mind with relation to evolution. The genes, that in a short period appear so stable, are found rather to be labile, though the changes require time. Through changes in the organization of the genetic system, very great numbers of diverse types arise, even during periods spanned by a human lifetime. Through changes in the genes themselves, other great numbers of diverse types arise; and these form a foundation for still further changes. Selective elimination plays an immense role in determining the general result of all these alterations of the inherited characteristics. These are matters of observation, not of theory. The general picture of what is happening has many features in common with Darwinism: the occurrence of many changes in the hereditary constitution, with natural selection operating on them. The great evolutionary transformations revealed by paleontology fit well with the rate of change in the genetic system revealed by experimental breeding.

NOTES AND REFERENCES ON CHAPTER XIV

1. Page 303. For details of many cases of changes in the organization of the genetic system, see T. H. Morgan, *The Theory of the Gene* (New Haven, 1926); and R. R. Gates, *Polyploidy,* British Journal of Experimental Biology, Vol. 1, 1924, pp. 153–182.

2. Page 306. For the role of changes in chromosome number in producing new varieties, see the references mentioned above; also C. B. Bridges, *Chromosome Aberrations and the Improvement of Animal Forms,* Journal of Heredity, Vol. 19, 1928, pp. 349–354.

3. Page 307. For the tendency of such varieties to reproduce without fertilization see the paper of R. R. Gates on Polyploidy, referred to in Note 1.

4. Page 308. For accounts of the remarkable investigations on changes of hereditary characteristics in the Jimson weed, see A. F. Blakeslee, *Variations in Datura due to changes in Chromosome Number,* The American Naturalist, Vol. 56, 1922, pp. 16–31; A. F. Blakeslee and John Belling, *Chromosomal Mutations in the Jimson Weed, Datura stramonium,* Journal of Heredity, Vol. 15, 1924, pp. 195–206; and A. F. Blakeslee, *The Genetics of Datura,* Verhandlungen des V. Internationalen Kongresses für Vererbungswissenschaft, Bd. 1, 1928, pp. 117–130. See also the numerous papers listed in these publications.

5. Page 311. For accounts of the relation of the numbers of chromosomes to changes of characteristics in the evening primrose, see R. R.

Gates, *The Cytology of Oenothera,* in Bibliographia Genetica, Vol. 4, 1928, pp. 401–492; with the references there listed.

6. Page 312. The breaking up of chromosomes and other changes in the organization of the genetic system by the action of X-rays are described by H. J. Muller and A. C. Dippel, *Chromosome Breakage by X-rays and the Production of Eggs from Genetically Male Tissue in Drosophila:* British Journal of Experimental Biology, Vol. 3, 1926, pp. 85–122; also H. J. Muller and T. S. Painter, *The Cytological Expression of Changes in Gene Alignment Produced by X-rays in Drosophila:* The American Naturalist, Vol. 63, 1929, pp. 193–200. The number for June, 1929 of the Journal of Heredity is entirely devoted to papers on this subject.

7. Page 312. See T. S. Painter and H. J. Muller, *Parallel Cytology and Genetics of Induced Translocations and Deletions in Drosophila:* The Journal of Heredity, Vol. 20, 1929, pp. 287–298.

8. Page 313. L. V. Morgan, *Non-crisscross Inheritance in Drosophila melanogaster,* Biological Bulletin, Vol. 42, 1922, pp. 267–274.

9. Page 314. Descriptions and figures of the chromosomes for the divers species of Drosophila are given by C. V. Metz, M. M. Moses and E. D. Mason, *Genetic Studies of Drosophila virilis; with Considerations on the Genetics of Other Species of Drosophila:* Publication No. 328 of the Carnegie Institution of Washington, 1923.

10. Page 316. See H. J. Muller, *Artificial Transmutation of the Gene,* Science, Vol. 66, 1927, pp. 84–87; and by the same author, *The Problem of Genic Modification,* Verhandlungen des V. Internationalen Kongresses der Vererbungswissenschaft, Bd. I, 1928, pp. 234–260.

11. Page 317. For accounts of the many different mutations in this gene, see H. J. Muller, *Further Changes in the White-eye Series of Drosophila and Their Bearing on the Manner of Occurrence of Mutation,* Journal of Experimental Zoology, Vol. 31, 1920, pp. 443–473.

12. Page 317. For detailed accounts of the gene mutations of Drosophila, see the list of publications by T. H. Morgan, C. B. Bridges, and A. H. Sturtevant, given at the end of Chapter II. An Alphabetical descriptive list of the mutations is given by the authors just named in *The Genetics of Drosophila,* Bibliographia Genetica, Vol. 2, 1925, pp. 217–239.

13. Page 316. See T. H. Patterson, *The Production of Mutations in Somatic Cells of Drosophila melanogaster by Means of X-rays,* Journal of Experimental Zoology, Vol. 53, 1929, pp. 327–372.

14. Page 319. See H. J. Muller and E. Altenburg, *The Rate of*

Change of Hereditary Factors in Drosophila. Proceedings of the Society of Experimental Biology and Medicine, Vol. 19, 1919, pp. 10–14.

15. Page 320. H. J. Muller, *The Problem of Genic Modification* (cited above), p. 247.

16. Page 323. Compare the discussion of the origin of diverse species in Drosophila by A. H. Sturtevant, in *The North American Species of Drosophila,* Publication No. 301 of the Carnegie Institution of Washington, 1921, pp. 121–122.

XV

ENVIRONMENT AND THE FUTURE OF THE RACE. INHERITANCE OF ACQUIRED CHARACTERS

WHAT effect has the nature of the present environment on later generations? What effect have our reactions to present conditions on the characteristics of our descendants? Present conditions and the reactions to them certainly affect later generations in at least two different ways. First, as we have seen in the preceding chapter, radiations of certain kinds may directly alter genes, giving origin to descendants having new hereditary characteristics. Second, stocks that live in the laboratory or under domestication leave descendants differing from those left by similar stocks that live in the wild. Under the mild conditions of the laboratory or of domestication, weak or defective individuals live and propagate, leaving many weak and defective descendants for future generations; while under the harsh conditions of nature no such descendants remain. Present conditions thus affect posterity directly, by altering the genes; and indirectly by selective elimination, by permitting certain types to multiply and preventing others from doing so.

These two effects of present conditions on future generations are solid realities, readily observable. One of the most popular theories of biology holds that there is a third effect of present conditions on descendants, less direct than the first one mentioned, more direct than the second one. Organisms react differently to different environments, so that they acquire different habits and different characteristics under different conditions. Many examples of this are given in our Chapters V and VI. The theory of "the inheritance of acquired characters" holds that after certain characteristics have been acquired as a reaction to particular conditions, later generations show a tendency to develop those same characteristics even without the condition that originally called them forth.

To what extent are these different methods of action at work? Is the third one—"the inheritance of acquired characters"—at work at all? What are their consequences for the later history of the stocks affected?

Direct Action of External Agents in Modifying Genes

Direct action of conditions on germ cells and genes occurs readily and frequently. But its usual result is not an effect on descendants produced by those germ cells, but merely the death of the germ cells. If it kills certain types of germ cells and not others, there *is* an effect on posterity, but an effect due to selective elimination, not to alteration of genes. The relation of direct alteration of genes to selective elimination is most difficult to disentangle. Sometimes they work together. Often a result attributed to one is due to the other. We shall see many examples of this.

Radiations

In the direct action of conditions on genes, the difficulty is to produce alteration without killing the genes. And for an effect on descendants, the genes must be so altered that as they grow and divide, they produce anew the altered constitution, not the original constitution. Radiations can do this, as we have seen. They operate on the genes individually. In several species of fruit-flies, in maize, in barley, and possibly also in the Jimson weed and in tobacco, gene mutations have been thus produced, giving rise to descendants with new inherited characteristics.[1] Many diverse genes are thus caused to change, and in ways closely similar to the mutations that occur without subjection to radiations. The mutations resulting from radiations are in the main, like other mutations, disadvantageous to the organism. They result in breeds with hereditary defects, and with decreased vigor and resistance. Selective elimination is here, as elsewhere, mingled with direct effects on genes. Many of the gene mutations result in the death and elimination of the mutated stocks. Whether advantageous mutations may result from radiation is as yet uncertain.

As mentioned in the preceding chapter, there is some evidence that the seemingly spontaneous mutations which occur in the laboratory or in nature are in fact due to natural radiations given off by radioactive materials in the earth's crust, or from other sources. Two investigations, by Babcock and Collins, and by Hanson and Heys, indicate decidedly that this is the case.[1] In these investigations, large numbers of fruit-flies were bred on the one hand in a region where there were few natural radiations; on the other hand, in a region where the amount of natural radiation was about twice as great. In both investigations, the number of mutations occurring was much greater in the region where the natural radiations was more abundant.

Such investigations need to be repeated many times before the conclusions indicated by them can be considered established. If they turn out to be correct it is difficult to exaggerate their interest and importance. They would seem to give a general answer to the question of the origin of hereditary changes in organisms. They would show that such hereditary changes are indeed brought about through the action of the environment. They open a method for the control of such hereditary changes; for preventing them, or for producing them at will. Within the next few months or years these matters will doubtless be positively settled.

Other Agents

Radiation acts with minute particularity, so that it may affect one gene and not its neighbor in the same cell. Most other agents have more general effects. May such agents, may high and low temperatures, chemical and nutritive conditions, and the like, likewise directly alter genes? The evidence with respect to other agents is much less clear.[2] H. J. Muller has found that the number of gene mutations occurring in a population of fruit-flies is slightly increased at higher temperatures. J. W. Heslop Harrison supplied certain moths with food containing metallic compounds. After some generations of this treatment, a certain number of darkly pigmented individuals were produced, and the descendants of these were likewise darkly pigmented, though not fed the food that induced this coloration. In later generations the dark color was inherited in the Mendelian manner. Such darkly pigmented breeds did not appear among broods that were not fed on the food containing the metallic salts. The metal had apparently caused a gene mutation. In the industrial regions of Northern England, where the air contains much smoke bearing metallic salts, various species of moths that were formerly light in color have become prevailingly dark. Harrison believes that this is due to alteration of the genes through the feeding of the moths on leaves covered with smoke containing the metallic salts. Standfuss and Fischer long ago reported that subjection of the larvæ of certain butterflies to very high or very low temperatures similarly causes the appearance of hereditary dark pigmentation.

Injury to Genes by Bad Living Conditions

A doctrine that has been much held is that bad living conditions injure the germ cells, giving rise to descendants that are degenerate, and that these effects are hereditary. To such action have been attributed many of the ills of humanity. Alcohol and other poisons, the products of over-fatigue and of diseases, the effects of under-nutrition—these are held to injure the germ cells (and presumably the genes), giving origin to the defective individuals that so abound in human populations.

What is the evidence on this? In examining it, one must remember that the germ cells carry cytoplasm as well as genes, and that poisons in the body of the parent might injure this cytoplasm in such a way as to make the individuals developed from these germ cells defective, without actual injury to the genes. In that case the children of parents that live under bad conditions might be defective, but if these children lived under good conditions, their offspring (the grandchildren) would be normal again. Or possibly such direct effects on the cytoplasm of the germ cells (without injury to the genes) might continue for two or three generations. But if the genes were uninjured, ultimately the stock would come back to normal.

This is a matter for experimentation. If animals and plants are kept under injurious living conditions, do defective offspring result? And if so, do the defects appear in later generations, even from parents that live under good conditions?

Many defective genes arise independently of conditions that are favorable or unfavorable for the life of the parents. In the fruit-fly, under ordinary conditions, hundreds of heritable defects have appeared, giving rise to a most degenerate posterity. Yet no characteristic difference in the living conditions is found between the parents in which the mutations occur and those in which they do not. Possibly (as has been suggested) some or all of these gene defects result from radiations coming from the earth or sky. But this is an all-pervading agency, occurring to the same extent in favorable and unfavorable conditions.

Thus under unfavorable conditions a certain number of gene defects will appear that would equally have appeared if the conditions had been favorable. One must be on guard against attributing these to the unfavorable conditions. This causes great difficulty, as we shall see, in interpreting the results of bad conditions. What we require to know is whether the descendants of parents that live under noxious conditions clearly show more hereditary defects than descendants of similar parents that live under favorable conditions.

The Protozoa

In the simplest organisms, the Protozoa, consisting of single cells, bad conditions may indeed induce hereditary degeneracy.[3] A. R. Middleton kept the protozoan Stylonychia at high temperatures for hundreds of generations. In later generations its vitality declined, so that its rate of reproduction decreased to less than one-fourth what it was at the beginning. If now the stock was restored to normal temperatures, and it was there compared under the same conditions with a stock that had not been kept at high temperatures, the lowered vitality was found to be inherited from generation to generation. Unfavorable conditions have induced hereditary injury. Similar effects were observed by V. Jollos when an infusorian was subjected for many generations to calcium nitrate. The rate of reproduction was lowered. When this stock was restored to normal conditions and compared there with a stock that had not been subjected to calcium, the depressed rate of reproduction was found to be inherited for a long series of generations.

A great number of such experiments have been carried on with the Protozoa, giving similar results. Unfavorable living conditions, continued for many generations, caused gradual depression, degeneration, which becomes greater and greater as generations pass. In many of these experiments the effect of restoration to normal conditions has not been tested, as it was in the experiments described above. In some cases restoration to normal conditions again produces, after many generations, a slow return to the high level of vitality, and this too is inherited. And there are other methods of restoring vitality in Protozoa.[3]

Higher Organisms

In the Protozoa the offspring are produced from the parents by a single cell division. In higher organisms, on the other hand, thousands of cell divisions are required to produce the developed individual. This difference appears to cause a great diversity between higher and lower organisms as to the production and inheritance of defects induced by environmental conditions. Yet even in higher organisms there are reports of congenital and hereditary defects that appear to be due to environmental agents which have acted on the parents. Some of the more important of these are the following:

Little and Bagg found among the descendants of mice that were subjected to X-rays some inherited defects that were not found among those not acted on by the rays. Yet only a very small proportion of the individuals acted on by the rays yielded the defective offspring. This confuses the interpretation. Were hidden defective genes perhaps already present in the stocks employed? Since we know from the work on the fruit-fly that X-rays do produce gene mutations, it appears not improbable that the hereditary defects observed in the mice were due to this cause. Incautious exposure to X-rays may result in serious injury to unborn generations.

M. F. Guyer found that introduction into rabbits of certain foreign serums was sometimes followed by the appearance of inherited eye defects in the descendants. Yet only a very small proportion of the individuals treated yielded the defective offspring (although from these few, many can be produced in later breeding), and careful repetition of the experiments by other investigators, on the same animals, and on others, yielded no defective progeny. This makes the interpretation of Guyer's results uncertain. Possibly hidden defective genes were already present in the stock, and their coming to light was quite independent of the introduced serum. Eye defects occur not uncommonly in rabbits, independently of such experiments.

Effects of Alcohol

More clearly defined, but still confusing, are the results of many experiments dealing with the effects of alcohol on posterity. D. D. Whitney, B. Noyes, and J. E. Finesinger [4] have kept lower organisms (Rotifera) for many generations under the influence of alcohol. This lowers their fertility, vitality, and resistance. On removing them from the alcohol the first generation offspring still have a lowered vitality (they are born of alcoholized parents). But in the next and subsequent generations, the injurious effect has completely disappeared. The alcohol has produced no inherited injury. These experiments must have very great weight in judging of this matter, since in these organisms uniform stocks could be employed (as they cannot in higher animals), and they were subjected to alcohol for great numbers of generations. The genes show a very great resistance to alcohol. Either it does not alter them at all, or it kills them; in either case no modified descendants result.

C. R. Stockard, on the other hand, found that in a considerable proportion of cases guinea pigs subjected to alcoholism give descendants that are weak or seriously defective, to the second and third generations succeeding the alcoholized parents. But in the fourth generation the defects have disappeared. This may indicate that the genes themselves are not injured, the effects being the result of the direct action of the injured parental bodies on the cytoplasm of the germ cells. Or possibly part of the genes were injured, and the individuals bearing the injured genes died out in the course of three generations; this appears to be Stockard's opinion.

These results appear of extreme practical importance, even though no permanently inherited defects were produced. Whatever its method of action, if alcoholism of parents produces defectiveness of offspring to the second and third generations (though no further), the matter is one requiring most serious consideration. Yet other experiments with vertebrates have not given such results. Pearl tested the results of alcoholism on fowls. He found that the descendants of alcoholized parents are not defective. Such parents produced fewer offspring than usual, but these offspring had a lower rate of mortality and a larger size than the descendants of parents not subjected to alcohol. This result appears due to selective elimination by the alcohol. It destroys the weak germs, thus yielding in the end less numerous but more vigorous descendants. After this work of Pearl, Stockard examined from the same point of view the descendants of his alcoholized guinea pigs. Though in the second and third generations the descendants were weaker and more defective than others, in the fourth generation they showed, like Pearl's fowls, a lower mortality rate than the descendants of parents not subjected to alcohol. Again selective elimination had occurred, removing the weaker strains. E. C. McDowell found that alcoholized white rats produced fewer litters and fewer young to the litter; but these offspring in turn produced larger litters, and the descendants in both generations were larger than the descendants of non-alcoholized stock. Selective elimination was again at work. Hanson and Heys have carried on similar experiments with rats. They find that none of the effects of alcohol are inherited, but again there are indications of selective elimination, the weaker germs being destroyed.

Thus in searching for the effects of injurious agents in modifying genes, the actual results are often found to be due to selective elimination of germ cells. Most of the seemingly inherited effects of alcohol are the result of destroying the less vigorous germs, resulting in preservation of the more vigorous individuals. Only the injuries observed by Stockard in the second and third generations of descendants are clearly due to some other kind of action; but as they persisted no further, it is doubtful whether the genes were modified. No permanently degenerate stocks were produced in this way.

But selective elimination through alcohol does not act in the same way in all organisms. Bilski found that in frogs, alcohol, in place of destroying the weak germs, stimulates them to develop. Alcoholized frogs produce more young than usual; but later many of the additional progeny die. Bluhm found in white mice, and Correns in certain plants, that alcohol tends to eliminate the female-producing germ cells, so that the proportion of male offspring is increased. The same effect follows in some plants from other unfavorable conditions. Danforth found in the chick that germs bearing a definite abnormality, brachydactyly (short toes), stand alcohol better than the normals. Alcohol eliminates the normals and retains the abnormals.

The results of the above experiments with alcohol are typical. To clear and definite questions nature declines to give clear and definite answers. But on the whole it appears that in organisms above the Protozoa the genes are remarkably well protected from injurious agents. Though the individuals bearing the genes are for many generations seriously affected, their genes usually remain normal. Radiations may reach and alter the genes without killing them. If other agents ever do this, the cases are apparently rare. Any effects on posterity are usually due to the fact that certain types of germs are killed, while others survive. Sometimes it is the weak germs that are killed, so that the remaining stock is more vigorous. Or particular types of germs may be eliminated, even the normals, leaving a larger proportion of abnormals. On the whole it appears improbable that any considerable proportion of the defectives found in a human or other population are the result of direct injury to the genes by bad living conditions.

Inheritance of Acquired Characters

Playing a much greater role in biological theory than possible direct injury to genes by bad conditions, is the doctrine that characteristics developed by the parents under the influence of particular conditions reappear in the descendants even without those conditions. This, the common form of the doctrine of the inheritance of acquired characters, starts from the well-known fact that diverse conditions cause individuals, even though they have the same genes, to develop or "acquire" different characteristics—different structures, functions, behavior. Even characteristics definitely inherited in typical Mendelian fashion are thus altered by conditions, as shown in Chapter V. The doctrine of the inheritance of acquired characters holds that by some means the development, or the possession, of these new characteristics by the parent affects the germ cells and genes, in such a manner that the descendants tend to develop these acquired characters, even under other conditions.

No other biological doctrine has led to sharper controversies than this one. While its upholders often assume such inheritance to be a matter of course, opponents have held it to be intrinsically absurd. A particular condition acting on the parents to produce a certain effect, would have to act on their germ cells in an entirely different way in order to produce in the offspring the same effect as in the parents. To assume that this occurs is unreasonable, it is urged.

Yet viewed from another point of view, the appearance of the same results in parent and offspring is not unreasonable. The germ cells, with their genes, form part of the parental body that is developing under particular conditions. It is known that the different parts of the developing body may affect each other in such ways as to cause them to develop harmoniously; this is particularly the case for cells that remain in an undeveloped condition for long periods, as do the germ cells. In many respects the developing body, including its germ cells, may be conceived as a unit, all parts sharing in the developmental processes. In those activities of organisms that are most readily studied—in behavior—the principle holds that a process gone through repeatedly and under stimulation later takes place more readily and without the original stimulus, yielding habits. There appears to be no *a priori* reason why this might not be expected in development as well as in behavior. If the body develops as a unit, each cell taking part in that development, we have the basis required for this method of action. After it has developed a certain way one or many times under the action of certain stimuli, a piece of that body, constituting a germ cell, would later develop in the same way without the same stimuli. Developmental habits are as readily conceivable as habits in behavior.

Many things in the structure and development of organisms suggest this method of action. In earlier chapters it has been shown that the same diversity of characteristics is induced in some cases by environmental differences, in other cases by genetic differences. The structures produced under certain environmental conditions are closely paralleled by structures developed under the influence of certain genes without those conditions. The impression is hard to resist that there must be some method of passing from production through environmental action to production through the action of changed genes.

In the Lowest Organisms

Whether this impression is correct or incorrect, whether developmental habits are indeed formed, resulting in the inheritance of acquired characters, is to be decided only by experimentation and observation. In the lowest organisms—those consisting of but a single cell—experimentation has shown that inheritance of certain reactions to environmental conditions is indeed a fact.[5] Under the action of certain physical and chemical agents, the organisms acquire an increased resistance to the agents that are at work, and this increased resistance reappears in their descendants for hundreds of generations after these descendants have ceased to live in the conditions that induced the increased resistance. Some of the characteristics shown by individuals therefore depend on the environment under which their ancestors hundreds of generations earlier lived. After other hundreds of generations in conditions which lack the modifying agent, the acquired resistance disappears; and it may be brought to disappear by certain nuclear changes in the organisms. The nature of the internal processes on which depend this acquirement, inheritance, and loss of induced resistance in the Protozoa are unknown.

In Higher Organisms

In higher organisms the great number of cell generations that intervene between the parent and the developed offspring greatly alters the situation as to the inheritance of acquired characters. Either the acquired characters are lost during the intervening cell divisions, or the situation is made so complex that decisive experiments are most difficult to carry through. Experiments on the matter in higher organisms usually yield negative results, or results of such a character that their interpretation is uncertain. In the absence of decisive and dependable experiments, judgment on the matter is often based on other grounds than careful examination of the evidence. The question regarding the inheritance of acquired characters is one that touches the springs of behavior, the ideals of conduct, in many ways. By a not unusual turn of affairs the ideals of conduct formed on other grounds react on the judgment of this question. If the results of the individual's reaction to the conditions are carried on to his descendants, then an improved environment, or an improved method of reacting to the environment, means an improved race. Advances in civilization mean advances in human nature. Degenerate parents yield degenerate offspring; sloth, vice, and crime in the parents predispose the offspring to sloth, vice and crime. The parents' acquirement of skill helps the offspring to acquire skill; the exercise of his senses or intellect sharpens the senses and intellect of his children; the practice of morality in the parent helps the children to practice morality. Thus according to this doctrine the nature and fate of the child are largely in the parents' hands.

Touching thus like a religious dogma the motives for good and evil conduct, this doctrine has aroused passionate and partisan interest. It inflames the zeal of fanatics. It becomes a subject for propaganda in which the end justifies the means. Its discussion abounds in fallacies, misrepresentation, and abuse. Opposition to it is represented as opposition to morality and to progress. In return, its opponents look upon advocacy by a man of science of the inheritance of acquired characters as a symptom of mental degeneration, as presaging the end of a reputation and a career; and they point to modern instances.

As to the state of the scientific evidence, the reader finds a perplexing situation. Morgan, the foremost investigator of genetics, tells us that belief in this doctrine is based not upon scientific evidence, but upon desire to pass one's acquisitions to one's children.[6] The commonplace assertion is that the inheritance of acquired characters is disproved; that no competent investigator harbors the doctrine; that the matter is out of court, no more to be considered. Yet the recent and present technical literature of zoology abounds in experimental investigations devoted to this question. Eminent authorities have been heard to assert that most biologists incline toward belief in the inheritance of acquired characters. Investigators summing up the evidence have affirmed that almost all experimentation directed on the matter supports the inheritance of acquired characters. Opposition to the doctrine, it is sometimes asserted, is due, not to scientific evidence, but to a reactionary desire to hold back social progress.

What is the secret of this conflict of assertion? Why is it that an experimenter who puts forward the claim that he has proof of the inheritance of acquired characters is classified in the "lunatic fringe" of biology?

Evidence against the Inheritance of Acquired Characters

There are grounds for the extreme skepticism with which such claims are greeted. Perhaps the chief ground lies in the obvious fact that in higher organisms certainly ninety-nine per cent of the parents' acquirements are not inherited. This is an impressive fact. It raises presumption against the other one per cent.

Equally powerful in the same direction is another fact. Genes for recessive characteristics exist for many successive generations in bodies that, owing to the simultaneous presence of a dominant gene, develop the dominant characteristics. The gene for red hair is often in a body that develops black hair, yet the recessive genes are not affected by the way the containing body develops. When, in a later generation, the recessive genes become separated from the dominant genes, they produce the recessive character in all its original purity. All routine breeding thus shouts against any effect on the genes of the way in which the body develops, or any effect of the presence of certain characteristics in the body that contains the genes. The great mass of facts included in this statement weighs heavily against the inheritance of acquired characteristics.

Again, experimental breeding does indeed show that a given stock, subjected for many generations to a changed environment, may become hereditarily altered, in structures, functions, or habits. This in the minds of some upholders of the theory settles the matter. It appears a demonstration of the inheritance of acquired characters. But it turns out that the ordinary operation of biparental reproduction may produce such results, quite without alteration of genes. In such reproduction new combinations of genes are continually produced, so that a given stock brings forth great numbers of different types of offspring, hereditarily diverse in structure, function and habit. Some of these flourish under one set of conditions, others under another set. Selective elimination makes its appearance; those that cannot flourish under the prevailing conditions disappear, and the stock is now made up only of those adapted to these conditions. In this way a given stock may gradually become adapted to high temperatures, or to low temperatures, or to a certain type of food or habitat. Yet this is accomplished simply by the production of many diverse combinations of germinal material, with automatic elimination of those that cannot stand the prevailing conditions. In the gross, results are produced that resemble those that would follow from the inheritance of acquired characters. Such action occurs constantly in nature, and to it most students of genetics attribute the phenomena for which the inheritance of acquired characters is invoked.

Most investigators in genetics have gone through a period of experimentation on the inheritance of acquired characteristics. The usual result is negative; the experiments lead nowhere, and are abandoned; no account of them is published. Extended researches in great number have been directed upon it. As a rule either there was nothing suggesting the inheritance of acquired characters; or whatever did suggest it was in fact a consequence of sporadic mutations or of the Mendelian formation of new combinations, with selective elimination.

False Alarms

False alarms have been frequent. Investigators have again and again reported the inheritance of acquired characters, only to have it later shown that the results were otherwise produced. In consequence they have come to suspect that other cases will have a similar issue. This view is strengthened by the obviously defective precautions and faulty reasoning of many persons who report demonstration of the inheritance of acquired characters. Some of the false alarms may be mentioned.

Griffith reported that rats kept on a table whirling in a certain direction acquire the compensatory habit of turning in the opposite direction, and that this tendency to turn in a certain direction is inherited. The report caused an enormous sensation. It turned out to be the result of a deceptive coincidence in certain cases, of ear disease with the effect of the whirling table.[7]

A still more enormous impression was made when the famous Russian physiologist Pavlov reported, in his lectures in America, that mice which had been trained to come at the sound of a bell inherited this habit. The assertion has since been withdrawn.[8]

Paul Kammerer[9] carried on for many years investigations on the effects of the parental environment on the descendants, in Amphibia. His results were that the inheritance of acquired characters not only occurs, but that it is common, that it is the rule. In many different sorts of characteristics, and in many details, environmental effects were inherited. The salamander that became yellow on a yellow background yielded descendants that became yellow even in the absence of a yellow background. If germ cells from a body that had not thus become yellow were transplanted to a body in which the yellow color had been induced, these germ cells acquired from the body the tendency to produce yellow, so that they yielded yellow offspring. Colors, structures, "instincts," reactions to particular agents—all acted in this way. Changes induced in them by environmental conditions were inherited. If the results presented by Kammerer were correct, the inheritance of acquired characters was overwhelmingly demonstrated.

Criticism was brought against Kammerer's methods and results. The very fact that inheritance of acquired characters was reported as common and obvious, whereas many other careful investigators had searched long for it in vain, raised doubts. There was carelessness in his methods of work, it was charged, of such a nature as to make his results unreliable. His books showed a tendency to confused general theorizing, at times of a self-destructive character. He employed methods of advertising, and a sensationalism of statement that seemed not compatible with scientific reliability. Many of those that examined his work distrusted his judgment as applied to a field of investigation that is most difficult and deceptive.

Yet in spite of all this, his work made a strong impression, until it was suddenly shown that the result of one of his important experiments had been falsified. Kammerer committed suicide. His entire work has been discredited.

All these things, and others of the same sort, have produced in the minds of biologists a strong presumption against the correctness of reports that the inheritance of acquired characters has been experimentally demonstrated for higher organisms. This state of mind is often characterized as hidebound prejudice; but it is in essence merely a reluctance to be gulled. After the same story has been many times repeated, one foresees its end from its beginning.

Supposed Cases of the Inheritance of Acquired Characters

Yet experiments claimed to show the inheritance of acquired characters in higher organisms continue to be put before the scientific world. J. W. H. Harrison [10] experimented on certain races of saw-flies that fed on a particular species of willow. They were compelled for some generations to feed on another species. This was done by leaving them, outdoors, for some years, in a garden where only this second species was available. When in later generations they were given a choice between the original species of willow and the one to which they had become accustomed, they all, without a single exception, chose the latter. Harrison holds that they had acquired a food reaction to the second plant, and that this acquired reaction had been inherited. Although the flies had been outdoors unwatched for a year or more at a stretch, and races were known to exist that feed naturally on this second plant, Harrison holds this to be "an incontrovertible case of the inheritance of acquired characters." In view of the great opportunities for error in an experiment carried on in this way, opponents are inclined to cite this as an example of the lack of critical care shown in the claims for the inheritance of acquired characters; they hold that the result cannot be considered evidence for any doctrine. Pictet and others have also given accounts of change of food habits in caterpillars of certain moths, when forced to feed on a new plant, and of the apparent inheritance of the changed habit.

Brecher and Dürken report experiments with the cabbage butterfly. By subjecting the larvæ to lights or backgrounds of diverse colors, the colors of the pupæ derived from these larvæ are changed. The first generation offspring of the individuals from these pupæ showed a tendency to develop the same color that had been thus induced in the parental pupæ—although they themselves were not subjected to the conditions that modify the parental color. These results have been confirmed by J. W. H. Harrison.[11] As pupæ of many diverse colors occur even under uniform conditions, there appears opportunity for a selective action that would account for the results.

The most striking recent claims for the inheritance of acquired characteristics arise from the experiments of Wm. McDougall on the rat.[12] McDougall trained rats to escape, by swimming, from a water tank so constructed that they must learn and habitually follow a certain course, if they are to escape. He continued this for many generations, recording the times required to learn the method of escape. The time required decreased in the later generations. McDougall holds this to be due to the inheritance of the effects of the acquirement of the habit in the earlier generations.

Coming shortly after the fiasco of Pavlov's similar experiments which had been supposed to show the inheritance of habit in mice, McDougall's interpretation of his results meets with skepticism. As McDougall himself puts it, biologists rather generally will say: "There goes yet another unfortunate fanatic chasing a will-o'-the-wisp that has misled so many. Let us hope that he will retain sufficient honesty and sanity to discover his error and to avow it as frankly as Pavlov has done."

Many other observations have been interpreted as indicating the inheritance of acquired characters in higher organisms.[13] Most or all of them can be otherwise interpreted. Whether they and the experimental results described above, are accepted as cases of the inheritance of acquired characters depends to a considerable extent on how far one holds the enormous mass of cases in which it is established that characteristics acquired are not inherited, to be evidence against such inheritance; and on how far one is influenced by the repeated instances of claims for such inheritance that were later recognized to be errors. Most biologists are influenced by both of these considerations. It is commonly held that the inheritance of acquired characteristics has as yet not been demonstrated to occur in organisms above Protozoa. And the conviction is growing that this is because such inheritance indeed does not occur and hence will never be demonstrated, in higher organisms. Direct action of certain agents on genes, resulting in gene mutations, that are usually injurious, has been demonstrated (as set forth in earlier paragraphs). But the supposed tendency of the germ cells to reproduce habits and other characteristics acquired under special conditions by the parent is a very different case.

Racial Change through Selective Elimination

There remains the indirect action of environmental conditions on future generations, through the destruction of individuals that bear certain genes or gene combinations, while others are allowed to live and multiply, the result being that under different conditions different types of descendants remain.

This method of action is a demonstrated reality. In the fruit-flies living in the laboratory, individuals showing mutations—even injurious mutations—live and propagate, giving rise to many stocks, having diverse sets of hereditary characteristics. Under natural conditions, on the other hand, most of the mutated stocks disappear, because the conditions are too hard for them; so that the descendants form an almost uniform stock, like their ancestors. Under domestication great numbers of diverse varieties of plants and animals, resulting from alterations in the genetic system, live and multiply; while under natural conditions most of them disappear. The conditions thus affect posterity through selective survival and elimination.

As we have seen, one often comes upon the results of selective elimination when searching for the direct effects of agents in altering genes, or for the inheritance of acquired characters. The racial effects of alcohol, we saw in earlier paragraphs, appear to be mainly the result of selective elimination; through this the directly injurious effect is supplanted by an improvement in the surviving descendants.

In many other cases when one examines the effects of particular agents on posterity, one finds that these effects result, not from direct action on the genes, but from selective elimination. The agent destroys individuals bearing certain types of genes, allowing others to develop, thus changing the inherited characteristics of the descendants. The more deeply one studies the effect of present conditions on later generations, the greater appears the role of this selective action. Certainly a large proportion of the consequences that have been attributed to the inheritance of acquired characters, or to the direct action of agents on genes, are in reality due to selective elimination.

Such selective action yields many different types of results, depending on what agent is at work; and also on what different classes of individuals are originally present. If organisms are subjected to an unusually high temperature, then individuals that cannot stand this temperature are eliminated. Those that can stand it live and produce offspring which inherit their power of resistance. Later generations therefore show a greater resistance to high temperature than did earlier ones. Any injurious agent thus tends to produce a population that can resist it—provided it does not destroy all the individuals at the beginning.

Similarly, if the conditions are made easier for organisms, individuals are permitted to develop that otherwise would not survive. These hand on to their offspring the peculiarities resulting from the genes that they bear, so that the characteristics of later generations are changed. If the individuals of a species are living continuously at a very low temperature, then all the individuals that exist will be such as can stand this temperature. If now the temperature becomes milder, this permits the survival of individuals that cannot resist low temperatures. These multiply, descendants inherit their genes, and in later generations there are present many individuals that cannot stand low temperatures. The hereditary characteristics of the race have become altered, through the cessation of selective elimination by low temperatures.

This method of action is rendered possible by the fact that ordinary reproduction from two parents produces great numbers of diverse combinations of genes, which yield individuals with different characteristics. Any particular type of environment permits the development and propagation of some of these types of individuals, but prevents that of others.

This method of action thus yields results that are most deceptive; results that are readily attributed to the direct action of environmental conditions on hereditary characteristics or to the inheritance of acquired characters. The experimenter on the effects of physical and chemical agents on organisms must be continually on his guard, or this will lead him to false conclusions. It is the very Mephistopheles of biological experimentation, filling it, if unrecognized, with chimeras and deceptions. In experimental material many diverse combinations are formed, diverse chemicals, diverse motions, diverse genes, diverse systems. Experimental conditions cause the elimination of some of these, while others persist. At the end the material before us has changed. The experimental agent appears to have worked a transformation; in fact it has worked only an elimination. If we do not see the details—the production of many combinations, the elimination of certain sorts—we shall enunciate laws of action, of transformation, that are delusive phantasms. Again and again this has happened in biological experimentation. Stock is subjected to given environment. After a few generations it is found to be changed; the change is inherited even upon restoration to the usual environment. We seem to have discovered the inheritance of acquired characteristics. And then selective elimination is found lurking beneath the surface, and we know not what we *have* discovered. But for it, the inheritance of acquired characters has been overwhelmingly demonstrated. It is the evil genius of the biological experimenter. To it are due the teleological fantasies of biology. To it are due specific false doctrines in many concrete fields of work. Wherever it experiments there is superabundant production, whether of motions, of chemicals, of genes, of germ cells, of individuals, so that only a part continue—there must the biologist beware, for in such does the demon of selective elimination lurk. Particularly in studies of the transformation of organisms by outer conditions does it play the master role.

Does Environmental Improvement Cause Racial Deterioration?

One special aspect of the consequences of selective elimination has deservedly aroused very great interest. It is illustrated by the action of alchohol. The direct effect of alcohol on individuals is to cause injury. But through its destruction of the weak germs, the injury is turned into racial improvement; the progeny of the alcoholized parents are on the whole superior to those from parents not subjected to alcohol. On the other hand, in the laboratory of heredity, the conditions of life for the fruit-flies are much more favorable than in nature. In the laboratory they live upon the best type of foods, are kept at favorable temperatures, protected from enemies and from injurious agents of all sorts. The result is that the population of fruit-flies in the laboratory of heredity becomes filled with the weak, the halt, the moribund, the abnormal, the monstrous. It abounds in families with reduplicated legs and abnormal abdomens, families with degenerate wings or no wings, families with imperfect eyes or with no eyes. It is a population that under natural condition could not maintain itself for a generation. Improvement of conditions for the individuals has meant deterioration for the race.

And as we examine other cases, this relation is met again and again. As conditions are made better for the individual life, weak and defective individuals are enabled to survive and propagate, individuals that under a severe environment would be eliminated. These hand on their defective genes to descendants. Thus defectives multiply and the stock degenerates.

Is this the invariable and inevitable result of improvement of living conditions? Must racial degeneration follow when living conditions are improved? Is this true for man as for other organisms? Does progress in civilization mean degeneration of human kind?

These questions have often been answered, Yes! Humanity too, it is set forth, is becoming filled with weak and abnormal individuals, persons with defective eyes, ears, teeth, bodies and minds. Mutations are occurring in man as they are in the fruit-fly. Most of them result in defects and abnormalities. As the conditions of life become more favorable, more and more of the defective individuals are preserved and allowed to propagate. The race becomes more and more degenerate.

If this relation is inevitable, then it is true that civilization is destroying the human race. For the person who believes that degeneration must increase in proportion as living conditions are improved, evil is transformed into good, good into evil. The action of selective elimination appears in this respect to be the reverse of that which would result from the inheritance of acquired characters. For the latter, an improvement in the environment means an improvement in the race. For selective elimination, an improvement in the environment means degeneration in the race.

The doctrine that improved environment means harm to the race has flourished much of late. The entire enterprise of improving the conditions of life, it is urged, is in the wrong direction. The public health workers, the social workers, the civilizers, are corrupting the race, are destroying it. By protecting us from our enemies, the bacteria and the viruses; by removing the sources of disease; by showing us how to avoid unfavorable conditions and to find favorable ones; in short, by bringing us and our environment into harmony, they are promoting the survival of the unfit; they are progressively filling the race with the weak and the degenerate, who must hand on their weakness and degeneracy to their descendants. This should all be stopped. Hygiene must be discouraged, disease must be given full swing. The improvement of living conditions must cease, must be undone, or the race is lost!

If we confine ourselves to the facts of selective elimination, this doctrine appears plausible. But when we examine certain other facts of biology it becomes paradoxical, improbable, impossible. All organisms, by unnumbered devices, protect themselves from enemies and obtain for themselves favorable conditions. Their daily, their hourly, occupation is the seeking of good conditions, the avoiding of bad ones. The public health worker, the social worker, the civilizer is not alone in the nefarious business of adjusting the organism to the environment; everybody is doing it. And everybody means our brothers the birds and beasts, our cousins the insects and worms and plants; it means all organisms. We ourselves have been doing this sort of thing for a hundred million years. It will be a hard habit to break, if we must break it.

And as we look at it, the difficulties become greater. Organisms find it a matter of necessity to defend themselves against agencies that would destroy them. All organisms *must* protect themselves against the injurious forces of nature: against heat and cold and wind and wet; against starvation and against over-eating; against unfit food and drink; against bumps and bruises and broken bones; against plagues and poisons. That's what life is; a struggle for existence. If any organism ceased to struggle, ceased to select its environment, ceased to protect itself—its kind would become extinct in a generation. So it is with man, with bird, with fish, with worm, with protozoan, with plant.

We cannot therefore hew to the line in this matter; we cannot stop this whole business of adjusting the environment to ourselves, of adjusting ourselves to the environment. Some sort of an accord, of a compromise, there must be, between the requirement that the race shall be kept strong by selective elimination, and the requirement that the individual must have an environment favorable to life. How can these requirements be reconciled?

To grasp the situation that confronts humanity, consider certain typical facts. In man, as in other organisms, there appear at times individuals whose genes are defective. This results in defective development. Hormones may be produced that are deficient in quality or quantity, or both; this results in further defects. If the thyroid secretion is defective, either from poor genes or poor nutrition, the individual fails to develop normally; it becomes a cretin, an idiot. If insulin is not properly formed, diabetes results. If the sex hormones are not normal, intersexuality or other discordant conditions follow. (See chapter IV.)

But chemical therapeutics discovers that disorders due to defective genes can be remedied, if we know the means, just as other chemical processes may be influenced. The consequences of a defective thyroid secretion are remedied by introducing the thyroid hormone with the food; the pitiful cretin becomes a normal human being. Lack of insulin is similarly remedied, by introduction of insulin from outside. The necessary chemicals can even be synthesized, made artificially, as recent revolutionary researches show. Wonderful possibilities are opened up by this work. Unfortunate human beings that must have suffered in misery, a burden to themselves and others, are made normal, useful, happy.

But consider now the further results of an enormous future development of synthetic chemistry, of chemical therapeutics. Defects in genes become as open to remedy as defects in nutrition. A defective thyroid product is replaced by manufactured thyroxin; the individual is restored to normality. But his genes are not changed; they remain defective; they are transmitted to his descendants. His descendants too must be treated with thyroxin. The genes of another individual are defective for the secretions of the hypophysis; of another for the suprarenal secretion; of another for the reproductive hormone; of another for insulin. Chemotherapy remedies all these defects—for these individuals. But their descendants, receiving the defective genes, must likewise come under the treatment of the chemist. In time the race thus accumulates a great stock of these defective genes. Every individual that receives them must be treated with one or more of the substitutes for the normal products of the genes. Each must carry with him an arsenal of hypodermic syringes, of vials, of capsules, of tablets. Each must remain within the radius of transportation of the synthetic chemical laboratory on which he depends. *This* is the result of remedying gene defects.

This picture is not an attractive one. Far better is the condition of the race in which, through lack of skill in synthetic chemistry, defective genes have been cancelled as they arise; so that each individual bears within himself, in his stock of genes, an automatic factory for the necessary chemicals.

Now, it is suggested that this is typical of the racial results of all sorts of improvements of conditions. Certain combinations of genes yield human beings that are more susceptible to tuberculosis than others. By protecting them from infection, by rest and food and open air life, these are saved. They propagate, they increase. Stocks specially sensitive to tuberculosis become more and more abundant. In time the increase of stocks prone to tuberculosis overcomes the results of better environment; tuberculosis increases. If this reasoning is sound, the final effect of the anti-tuberculosis campaign must be bad.

And there is no ground for restricting this reasoning to tuberculosis. All diseases, defects, and weaknesses are affected by genes; their occurrence under given conditions will be altered by changing the gene combinations present. This is true for cancer, for feeblemindedness, for insanity, for criminality. Probably it is to some extent true for even such diseases as typhoid fever and pneumonia. It is maintained therefore that the general effect of so improving conditions as to lessen these diseases is to save weak and susceptible individuals that would otherwise be eliminated. The more the conditions are improved, the worse becomes the human stock. Man has been at this practice of saving defective genes for thousands of years—through the invention of fire, of houses, of clothing, of tools, through improved nutrition, through hygiene, through the art of medicine, through the advance of invention and of science.

How is this situation to be met? Two plans of procedure are put before us. If the bad condition of the race is due to improvement of the environmental conditions, then logically we should undo the improvements; we should go back to the situation before conditions were improved.

But how far back shall we go? Shall we stop measures of public health? Shall we go back to the hygienic conditions that yielded smallpox and plague, and the other epidemics that swept away half of the population? Shall we give up clothing, houses, fire? There has never been an invention that did so much toward conserving weak individuals as bringing fire into the service of man. Shall we stop increasing our knowledge of nutrition in man; shall we sweep away the knowledge already gained? At the present time the progress of science is the most effective agency in ameliorating the conditions, so that types of individuals are permitted to survive that formerly were eliminated. Shall we stop the progress of science?

It requires only an enumeration of these things to show that this method of action is not a practicable one. Man is a creature that does improve the conditions under which he lives, as do squirrels, ants, crayfishes and all other organisms. If this means ultimate destruction of the race, then ultimate destruction is certain.

Need for Eugenic Measures

But there is another way of meeting the situation. Improved conditions do not cause genes to become defective; they merely preserve and perpetuate genes that have become defective from other causes. What is required then is to stop perpetuating the defective genes. Continue with the improvement of conditions, that the individual's life may be successful and happy. The lives of even the individuals bearing defective genes may be made as satisfactory, as complete, as the most advanced civilization can make them, without the smallest harm to posterity; but these individuals must not propagate. It is not the preservation of individuals with defective genes that is harmful, but their propagation.[14]

What the situation demands therefore is that we shall learn how to recognize defective genes, and that we shall see that the bearers of these genes do not produce offspring. This is the program of eugenics. With this program we have dealt in Chapter X.

What are the prospects that eugenic measures can prevent the degeneration of humanity into such a condition as is found in a laboratory population of mutated fruit-flies? One feature of the comparison is most hopeful. In the population of fruit-flies, not only have defective individuals been permitted to live, they have been selected; while the normal individuals, unmutated, have been rejected, have not been allowed to propagate. Selective elimination has been reversed in direction, eliminating the normal, conserving the defectives. It is to this that the prevailingly abnormal constitution of the laboratory population is due.

Nothing of this sort has occurred or is occurring in man. The difference is fundamental. It encourages us to hope that if measures are indeed taken to prevent the multiplication of individuals with defective genes, the human race need not deteriorate. And this hope is further promoted by the fact that the human race still exists and is vigorous, after unnumbered ages of improving the conditions of existence.

NOTES AND REFERENCES ON CHAPTER XV

1. Pages 330 and 331. On the production of gene mutations by radiations, see H. J. Muller, *Artificial Transmutation of the Gene,* Science, Vol. 66, 1927, pp. 84–87; also by the same author, *The Production of Mutations by X-rays,* Proceedings of the National Academy of Science, Vol. 14, 1928, pp. 714–726. For the action of natural radiations in producing the so-called spontaneous mutations, see E. B. Babcock and J. L. Collins, *Does Natural Ionizing Radiation Control Rate of Mutation?* Proceedings of the National Academy of Sciences, Vol. 15, 1929, pp. 623–628; also F. B. Hanson and F. Heys, *A Possible Relation Between Natural (Earth) Radiations and Gene Mutations,* Science, Vol. 71, 1930, pp. 43–44.

2. Page 332. On the production of changes in the genes by the direct action of external agents, aside from radiations, as well as on the inheritance of acquired characters, see the review by J. F. Detlefsen, *The Inheritance of Acquired Characters.* Physiological Reviews, Vol. 5, 1925, pp. 244–278. In this will be found references to many other papers on the subject. See also J. W. H. Harrison, *A Further Induction of Melanism in the Lepidopterous Insect Selenia bilunaria Esp. and its Inheritance.* Proceedings of the Royal Society, B. Vol. 102, 1928, pp. 338–347.

3. Page 334. For a general account of these matters in the Protozoa, with reference to all the literature, see H. S. Jennings, *Genetics of the Protozoa, in Bibliographia Genetica,* Vol. 5, 1929, pp. 105–330.

4. Page 335. See J. E. Finesinger, *Effect of Certain Chemical and Physical Agents on Fecundity and Length of Life, and their Inheritance, in a Rotifer, Lecane inermis Bryce.* Journal of Experimental Zoology,

Vol. 44, 1926, pp. 63–94. This gives references to other papers on similar investigations.

5. Page 340. For inheritance of acquired characters in Protozoa, see the reference given in Note 3, above.

6. Page 341. For recent discussions of the inheritance of acquired characters (pro and contra) see T. H. Morgan, *Are Acquired Characters Inherited?* The Yale Review, July, 1924 (against); Paul Kammerer, *The Inheritance of Acquired Characteristics* (New York, 1924), 414 pages (for their inheritance); H. S. Jennings, *The Inheritance of Acquired Characters,* The Forum, November, 1926.

7. Page 344. See the paper of Detlefsen, referred to in note 2, above.

8. Page 344. See the paper of McDougall referred to in note 12, below.

9. Page 344. See the book of Kammerer, referred to in note 6, above.

10. Page 345. See J. W. H. Harrison, *Experiments on the Egg-laying Instincts of the Saw-fly, Pontania Salicis Christ., and their Bearing on the Inheritance of Acquired Characters; with some Remarks on a New Principle in Evolution.* Proceedings of the Royal Society of London, B, Vol. 101, 1927, pp. 115–126.

11. Page 346. References to the papers mentioned are given in the paper by J. W. H. Harrison, *Induced Changes in the Pigmentation of the Pupae of the Butterfly Pieris rapi L. and their Inheritance.* Proceedings of the Royal Society of London, B, Vol. 102, 1928, pp. 347–351.

12. Page 346. Wm. McDougall, *An Experiment for the Testing of the Hypothesis of Lamarck.* British Journal of Experimental Psychology, Vol. 17, 1927, pp. 267–314.

13. Page 347. For a compendium of the older cases held to be evidence of the inheritance of acquired characteristics, see R. Semon, *Das Problem der Vererbung "Erworbener Eigenschaften,"* Leipzig, 1912, 203 pages.

14. Page 356. For a further discussion of these matters, see the author's paper, *Public Health Progress and Race Progress—Are they Incompatible?* Science, Vol. 66, 1927, pp. 45–50.

XVI

DIVERSE DOCTRINES OF EVOLUTION: THEIR RELATION TO THE PRACTICE OF SCIENCE AND OF LIFE

We have dealt, in the chapters just preceding this, with such of the processes in the evolution of organisms as have thus far been established by experimental biology. There we saw that the hereditary constitution of organisms is not static, unchanging. We saw that organisms alter in their inherited characteristics; that races with new hereditary characters appear. We saw some of the internal processes, in the genes and in the chromosomes, that underlie these changes. And we saw that the agent producing these changes consists, in many cases at least, of invisible radiations; so that the suggestion has been made that such radiations are the cause of organic evolution.

But it is clear that the radiations do not decide the direction and nature of the evolutionary changes. One gene struck by a ray produces a change in the color of the eye; another a change in stature, or in the form of the limbs, or in the working of the brain. Diverse evolutionary changes produce organisms of different kinds. What is it that causes one line of evolution to produce insects, another to produce man? What indeed is the nature of the changes that have such results? What kinds of changes are occurring in the evolutionary process?

With the detailed steps that result in the production of particular kinds of organisms we shall not deal. Little is known experimentally of these; and their treatment from other points of view would require volumes. But certain general questions as to the nature of evolutionary change may be appropriately dealt with in this final chapter; for the answer to these questions bears directly on the theory and practice of science and of living.

Two main divergent views exist as to the nature of evolutionary changes. One of these looks upon evolution as the calculable working of a vast machine, operating by fixed and unchanging laws, so that nothing arises from it that was not essentially predictable from a knowledge of what had gone before. The other holds that evolution is creative; that in its operation essentially new things and new methods of action emerge, not calculable nor predictable from what had gone before. The former is the doctrine of mechanical evolution; the latter that of emergent evolution.

The clash between these doctrines is connected with the seeming conflict between the principles by which human life is regulated in the relations of men with each other, and the principles of scientific method. One represents the purely physico-chemical point of view, which commonly sets itself forth as that which is distinctly scientific; while the other represents more nearly what might be called the humanistic point of view. We propose to examine these two doctrines, with relation to the question: Which is the better guide in science and in life?

The two divergent doctrines have arisen from fixing attention primarily on one or another of certain kinds of changes that can be observed, and holding that one represents the type to which all changes conform.

Mechanical Evolution

The most obvious changes to be observed are the movements of parts of the world with reference to each other, with the resulting alterations in the arrangements of parts. Objects and organisms move from place to place; seas and continents alter their positions, mountains are leveled, plains elevated. Living things grow, change form and structure. The parts of objects and organisms move with relation to each other. The more minutely things are examined, the more universal appears this relative movement of parts and the greater the role that it plays. Such motion prevails among the most minute constituents of things; among chromosomes and genes; among molecules, ions, atoms, electrons, quanta. The consequences include many things that are not at first recognizable as motions or changes of arrangement; that are discovered to be such only by penetrating study.

So universal and so unexpectedly great in consequences are changes of this type that a large group of students of nature have been led to the conviction that this is the only kind of change that occurs. The universe has parts and these parts move with relation to each other, taking many different relative positions. This is the whole story! All details are but variations of the movements and the resulting arrangements of the parts. All evolutionary change is of this character. All science consists in the discovery of the laws of these movements, and of the varied arrangements consequent on them. Essentially this is the doctrine of mechanism, of mechanical evolution.

The conviction that all changes are of this character, when combined with the results of the detailed study of the movements and their consequences, leads to further conclusions of great moment; conclusions that determine the entire outlook on life and the world. For when the parts and their movements are examined, the motions are found to follow clearly-defined rules. General laws of motion can be deduced, showing the dependence of the motions on certain properties of the parts, particularly on their mass, on their relative positions and distances, and on the motions that are already in progress. These laws are found to hold under greatly varied conditions. It is concluded that they must hold under all conditions; a conclusion that has enormous consequences. The properties, the motions, the distances and directions, can be expressed quantitatively and subjected to mathematical treatment, so that the laws become mathematical formulæ. Thus from the masses, and the present arrangements and motions, it becomes possible to compute what the future motions and arrangements will be.

Such computation proves itself enormously powerful and useful. By it the courses of planets and stars, the courses of atoms and electrons, are explained and predicted. By means of it engineering projects are carried through. Through such computation and prediction man establishes mastery over much of nature. The examination and formulation of these matters is what constitutes (it is held) the sciences of physics and chemistry.

To certain parts and changes of the universe this method of computation and prediction has not been successfully applied; notably is this true for organisms. But this is held to be due to the present incompleteness of science. When sufficient data are collected and sufficiently complex computations are carried out, it must be possible to apply the same method to organisms. Since the universe is composed only of parts and motions and arrangements that can be expressed quantitatively, and since the motions occur always in accordance with the same laws, eventually the same method of computing and predicting results can be applied to the entire universe. From a knowledge of all parts, their arrangement and motions at a given time, all that will happen in the future could be successfully computed. By a sufficiently able computer the entire course of evolution could thus be correctly predicted.

According to this view then, the universe is a physicochemical mechanism, operating with invariable laws, its entire operation calculable in advance. Further operations, future existences, are as definitely determined as are present and past ones; they are merely waiting to be realized.

From these positive conclusions as to how the operation of the world is determined, flow certain negative conclusions, as to how it is *not* determined. Since whatever happens is determined by the pre-existing masses and motions and arrangements, it follows that ideas, opinions, purposes, ideals—all that we call mental—have no influence on the course of events; for such things are not masses nor motions nor arrangements, and cannot be taken into the computations by which things are predicted. Things mental have no role in the operation of the universe, no role in evolution. And since according to the mechanical view, all action is predetermined by the foregoing physico-chemical situation, in such a way as to be calculable from it, it follows that there is no possibility of *our* altering what will happen. For this was predictable before *we* came into existence. We are not agents; we are merely stages in the working out of the world-formula.

Furthermore, since the laws of nature are discoverable at any early epoch, and are immutable, the world must continue to act in the future as it has in the past. Nothing new in principle can appear. No new methods of action can come into operation. The thing that has been is that which shall be, and that which is done is that which shall be done, and there is no new thing under the sun!

Emergent Evolution

A second group of observers has been deeply impressed by another type of change; one that goes on in organisms. Each of us is an organism. And we find going on in ourselves certain changes that are not expressible by formulæ that include only masses and motions and arrangements. We discover in ourselves a sensation of pain, and this changes into one of pleasure. We have now a sensation of blue, then one of red. We harbor an opinion, which later transforms into another opinion. Thousands of such changes occur.

Computations that begin with masses, motions, arrangements, yield only other masses, motions and arrangements. They do not yield pleasure, pain, blue, red, opinions, ideas. Changes in these latter things occur simultaneously with motions, with changes of arrangement, but the only way that this can be discovered is by observation, by experience, not by computations from the motions and arrangements.

There is evidence that changes of the sort just mentioned are widely distributed, and have gone on for long periods. There exist other human beings that arose, not long ago, from pieces of the same individuals that we came from. We cannot directly experience their sensations, feelings, ideas, but there is no reason to suppose that they lack such—since they are pieces of the same material as ourselves. And they act as we do when we experience particular sensations or feelings or ideas. Furthermore, besides our fellowmen, there are other pieces of the same material as ourselves, that separated from us long ago. These are the other organisms. Many are much like ourselves: apes, dogs, birds. Others, as we pass down the scale, are less like us, till we arrive at such creatures as crabs, oysters, jelly-fish, plants. Many of these other creatures behave as we do when experiencing certain sensations, emotions and the like. Since they are indeed pieces of the same material as ourselves, there appears no ground for denying that they too have such experiences.

A great class of beings then seemingly has experiences of this type, goes through changes of this sort. Certainly each of us does; and each of us is a part of the universe, not to be omitted in summing up what the universe includes. Changes in these inner experiences must then be included among those that occur in the universe. Calculable motions of particles and changes in their arrangements are then not the only changes that occur!

These inner experiences and changes must be different in the lower organisms from those that we find in ourselves. The oyster certainly has not the richness of mental experiences possessed by Goethe or Shakespeare. Such mental experiences have therefore altered, developed, in the process of evolution. Their development is as much a part of the evolutionary process as are the changes in arrangements and motions of particles.

And as we look deeply into the past history of the world, it appears that there was a time when sensations, feelings, ideas, and the like, did not occur; for the conditions required for their occurrence did not exist. The possibility, indeed the great probability, must be reckoned with, that such things developed from a preëxisting situation in which they did not occur. A great class of things, in that case, arose, emerged, in the process of evolution—things that could not have been predicted by computations based on what existed before this class of things arose. Changes of this kind are what is meant by emergent evolution.

Even after the mental phenomena had emerged, they were certainly at first very different from those that are now discovered in man. They have transformed, developed, produced new kinds that did not before exist. All this transformation of mental phenomena as ages pass exemplifies emergent evolution.

The second group of observers holds that all this must not be left out of account. Changes of this kind, "emergences," are as much a part of evolution as are changes in motion and arrangement of particles. To the student of organisms, of human beings, these things are of the greatest interest and importance; in man they play a very great role. A view of evolution, a view of the universe, that omits them, is most inadequate and unsatisfactory. Emergent evolution must be accepted for the development of things mental.

And what relation have such changes to the type of changes dealt with by mechanism; to changes in motion and arrangement of particles? Do changes in matter and motion affect mental changes? Do mental changes affect the motion of particles and masses?

How are we to discover the answer to these questions? Critical observation and experimentation are the final foundations for science. To straightforward observation and experiment it appears that each of these kinds of change affects the other. We experiment with heat and cold; they yield different sensations. We drop a heavy weight on the foot. This yields a very different sensation from that experienced when this physical change does not occur. Infinite in number are such relations between physical and mental changes; life is largely made up of them. And no matter how refined the technique, no matter how critical the experimentation, it is found that physical changes give origin to mental ones. This must be accepted as a part of experimental science.

This conclusion is revolutionary, so far as the computability of the results of physical changes are concerned. In addition to the computable motions and arrangements, there emerge uncomputed sensations, emotions, thoughts, and the like, in infinite variety. This too is the nature of change!

Still more revolutionary in its bearings, particularly on the nature of evolutionary change, would be the conclusion that incomputable sensations, feelings, ideas, and other mental changes, alter the physical processes, alter the motions and arrangements of particles; that they affect behavior. To the natural man it appears that they do. When I receive pain from an object I withdraw from it; if I receive pleasure, I do not. When I hold one opinion, I take certain action; if that opinion is changed, I act differently. It seems to me that my sensations, feelings, ideas, purposes, thoughts, affect largely what I do.

But the mechanist is alarmed at this conclusion. If such things affect motions, the computability and predictability of events are lost. His computations do not include sensations, feelings, thoughts. If these things alter the result, the computation must yield incorrect conclusions. Something occurs that his computations did not indicate.

The mechanist is unwilling to give up this computability and predictability of all that happens. To him it appears that this is the essential feature of science; that to give it up is to give up science. And so he resists the notion that sensations, feelings, ideas, purposes, have anything to do with what happens. He holds that the conclusions of the natural man are uncritical. The mechanist points out that when a sensation arises, there is a characteristic physical change also. The material situation alters, outside or inside the body of the organism (or both). It is to this physical change that he attributes the movement which the natural man ascribes to the sensation. When I withdraw my hand from a hot object, it is to the physical change in my hand and my nervous system that he ascribes the withdrawal of my hand; not to the sensation. This type of explanation he applies to all cases of apparent efficacy of mental processes; to all the seeming effects of diverse sensations, feeling, emotions, ideas, opinions. He points out that the advance of investigation tends to establish that all mental processes are accompanied by physical processes, that all differences in mental states or mental changes are accompanied by characteristic differences in physical processes. No class of mental change is known that occurs without change in physical condition. No case of a mental change without a physical change is established. The further investigation goes, the more complete becomes the demonstration that diversities of mental and physical processes go together. He believes therefore that this is universal.

Accepting this, the mechanist attributes all the supposed effects of diverse mental processes to their accompanying diverse physical processes. All these physical changes and their physical consequences are held to be computable, predictable. Although the mental state or change was not computable from physico-chemical data, everything else that happens *is* thus computable. Therefore the sensations, feelings, ideas, opinions, purposes, have no influence on the results; have no role in what goes on in the world, in the movements of objects or the behavior of human beings. The same physico-chemical conditions without the mental states, he holds, would produce the same results.

How are we to discover whether the natural man or the mechanist is right in his conclusions? Again we must turn to experiment, the final arbiter of all questions in science. To discover whether it is the given physical situation or the given mental state that produces the result, we must isolate them; we must remove one, leaving the other unchanged. We must try the same mental state without the characteristic physical situation. We must try the same physical situation without the mental state.

But when we propose this we discover it to be an impossibility. No such experiment can be tried. The situation on which the mechanist has based his claim is, that when there is a sensation, there is a characteristic different physical condition from that in which the sensation is lacking; that to every difference in mental state corresponds a difference in physical situation. One cannot, therefore, remove or alter the sensation except by altering the physical situation. And one cannot alter the physical situation without removing or changing the sensation or other mental state. There is then no experimental ground, there can be no experimental ground, for the assertion that the same physical condition will produce the same result without the mental state. Such an assertion is metaphysical, unscientific, without meaning. It is in exactly the same position as the assertion that the mental state without the physical situation would produce the same result; that is, it is utterly without foundation. There is no scientific ground for attributing the result that is brought about to either one of the two factors (mental or physical) to the exclusion of the other. They are inseparable; experimentally and practically they are identified.

And since they are inseparable, identified, the specification of either implies the other. They are two names for one situation. It follows that either may be employed in describing the results of experimentation. The outside observer, experimenting by physical and chemical methods on a human individual, may without error attribute the results of his experimentation to the physical and chemical conditions, provided that he refrains from asserting that the mental state has no role. He may do this, because the mental state has its characteristic accompanying physical situation, different for every diverse mental state; so that there never lack diverse physicochemical conditions for every difference in results. There is always an objective experimental cause for every change that occurs. There is no obstacle to a full objective experimental analysis for all objective processes.

The same situation holds for the humanist who is interested in the way in which opinions, prejudices, emotions, sway human behavior. He may without error attribute what happens to these mental states, provided he does not attempt to divorce them from the characteristic physical conditions from which they are inseparable. There is no possible experimental ground, no scientific ground, for denying efficacy to sensations, emotions, ideas, opinions, thought, provided it be admitted, as it is by the mechanist, that each of these has its characteristic different physico-chemical condition. If the sensation, the emotion, the idea, is taken away or changed, the following action is changed. This is precisely experimental determination of the action by the mental state. The only escape from this conclusion would be the proof that, in the situations that go with definite diverse mental states, all the parts move in accordance with identically the same laws of motion that they do in other situations in which no mental state occurs. Not the faintest beginning of such a demonstration has been made; there is no indication that it ever will be made. The emergent evolutionist is free to believe that when specific mental states occur, the rules of motion of the parts are different from those prevailing when no such mental state occurs.

Thus the emergent evolutionist holds that in the course of evolution there have emerged things that are new, of a different kind from anything that has gone before; and that are not predictable from a knowledge of the preëxisting things, from a knowledge of the preëxisting particles, their arrangements and motions. And at the same time the methods of movement of the particles change, so that the later motions and arrangements are no longer predictable from knowledge of previous motions and arrangements. New laws of motion, new methods of action, have appeared, as new arrangements of particles occur, and particular mental states arise. And this is continuing as evolution proceeds, at present as in the past.

All this he holds is obvious for organisms. It is true for the development of individuals; for the development of their mental experiences and for the development of behavior that goes with them, as exemplified in one's own self—a typical organism. And it is true for their evolutionary development through past ages.

And the emergent evolutionist may take a step farther, a large step. Chemical properties have in the overwhelming majority of cases not been computed or predicted from the motions and arrangements of electrons, from the properties of the particles taken separately. Like the peculiarities of organisms, they are learned by experiment. To the emergent evolutionist this appears significant for the nature of things. He holds that probably new properties, new modes of action appear as the arrangement of parts are changed, even in the inorganic. He holds this with less confidence for the inorganic than for organisms; but he holds it until the contrary is shown.

Thus the typical doctrine of emergent evolution holds that new properties and modes of action appear when the steps are made from atoms to molecules, from simple molecules to complex ones, from inorganic to organic. It holds that the properties of atoms do indeed depend on those that the electrons have *when they are in the atom;* the properties of molecules on those which the atoms have *when they are in the molecules.* It holds too that the properties of living things depend on those of their physico-chemical constituents *when the latter are in living things;* the activities of thinking beings on the action of their physiological constituents when the latter are part of a thinking being; the activities of societies on those of their unit individuals when those individuals form part of society. But it holds that the constituents of each grade acquire new properties, new modes of action, in becoming part of the emergent thing of higher complexity. It holds that the physics of atoms, of molecules, is not fully known till these are studied in the living as well as in the non-living. It holds that the physiology of bodily constituents separated from the living organism is in essential respects diverse from their physiology in the living organism. The constituents of the emergent thing partake of the properties which they showed before becoming parts of that thing, but with additions and modifications. The properties of the emergent unit do indeed depend on the properties of its constituents; but it is on their properties as altered by becoming part of the emergent unit. The parts depend upon the whole, as well as does the whole upon its parts.

Consequences for Science and for Life

What difference does it make if we accept the doctrine of emergent evolution, rather than that of mechanical evolution?

It makes a very great difference. It makes a difference in the object and the practice of science; in the temperament and bearing of the man of science; in the relation of science to life; and in one's general outlook on life and the universe.

Look first at its relation to the object and practice of science. For mechanical evolution the ideal scientific method is mainly rationalistic, to but a minimal extent empirical. From the examination of any small part of the universe, at any time, it is possible to discover the laws of action, of grouping, for all its parts and for all periods. Only a few preliminary observations should be required—of the particles, their arrangements and motions. The rest is a matter of computing, of reasoning. Science should quickly leave its toe-touch with observation and soar away in mathematical calculations, in philosophical reasonings. From a sample of the universe we ought to be able to reason out the rest. Continued recourse to experimentation is but a device of feeble minds; an attempt to discover in a rude manner what we should know by calculations and logic.

For the doctrine of emergent evolution, on the other hand, observation and experiment are the primary and the final methods of science, never to be laid aside. They are *the* methods for learning of the universe. On the basis of what they bring forth, reasoning, computation, may indeed act, so long as these stay within the restricted circle that shows nothing new, nothing emergent. But always there is the possibility that emergents have come into the circle; always the conclusions must be tested by experiment. The new things, the new modes of action, that come in evolution, cannot be discovered by reasoning, but only by observation and experiment. The man of science must accept as the final word John Hunter's maxim: Don't think; try! Thinking is an instrument, a very fallible instrument, for helping to decide what to try, but the last word must be *try*. Science is the organization of *experience;* what shall go into it is entirely a matter of experience.

The doctrine of emergent evolution makes no difficulties for experimentation, for the experimental dependence of all that happens on preceding conditions. It is as things come into new arrangements, new relations, that their properties and actions change. There is always an experimental cause for every change that occurs. It offers no obstacles to the continued progress of science nor to its formulation. At the same time it sets no limits as to what science may discover. It recognizes that science is never finished; that it must continue to develop as long as evolution continues.

The doctrine of emergent evolution makes a great difference to one's conception of the relations between the living and the non-living, to one's view of the relations between the sciences that deal with the inorganic, and those that deal with the organic. It rejects the prevalent dogma that the only sound method of learning about the organic is to study the inorganic. It repudiates the notion that the best interpreter of the living is he who confines himself to the study of the non-living; a notion that has been the curse of biological science, condemning it to move in pretentious superficialities. Emergent evolution does indeed demand a study of the inorganic as well as of the organic, but the former is no more essential than the latter. It demands a study of the inorganic, for the understanding of the organic. Since the activities of constituent parts in the living are modifications of their simpler activities in the inorganic, and since many of the simpler actions persist too in organisms, a knowledge of the inorganic must continue to be the foundation on which to build an understanding of the organic. But the constituent parts act differently within the living creature, for they have come into different relations. Experimentation is as valid and as indispensable in the living as it is in the non-living. Any result that it yields in the living is as sound and may be as ultimate as anything it discovers in the non-living. The doctrine of emergent evolution makes the biologist loyal to the results of observation and experiment in his own field of work, whatever is found in other fields. Biology becomes a science in its own right—not through rejection of the experimental method, but through undeviating allegiance to it. The doctrine of emergent evolution is a declaration of independence for biology.

And within the realm of biological science a parallel result follows. Different organisms, different societies of organisms, are diverse emergents, showing diverse systems of relations, and consequent diverse methods of action. No longer must it be held that what is true for one organism is necessarily true for another. No longer will the investigator expect by a single crucial experiment to settle a question for the whole organic world. Knowledge of the biology of the oyster is practically not a sound basis for judgment of that of the social insects; this practical fact will be recognized as theoretically significant, as a fact typical of biological science, not something to be minimized and explained away. Organic evolution will be seen as emergent evolution in its most conspicuous and manifold display. When this is recognized, the practice of facile generalization which honeycombs biological science with error will lose its seductive charm. To generalize will be recognized as the most laborious task in biology, instead of the lightest and simplest. To discover what organisms have in common becomes an object for wide-extended comparative investigation; not a matter for assumptions. Divergent results of experimentation in different organisms are not to be rejected on *a priori* grounds; diversities are as significant as uniformities. This state of affairs, which on the one hand is a corollary of emergent evolution, is revealed on the other hand by the advance of experimental biology; things living behave as if emergent evolution were a true doctrine.

And all this applies to man as to other organisms; to his conduct, to his social organization, to his prospects and possibilities. Man, like other organisms, is an emergent. His actions may follow the same principles as those of other organisms, or he may act on different principles. This is not a matter for assumption; it is all a question of fact, to be discovered by experiment, by experience, and in no other way. What man has in common with other organisms is to be discovered by investigation and careful comparison, not taken for granted. Wherein he differs from other organisms, wherein he is unique—this stands on the same footing; it is purely a question of observable fact. Data drawn from the study of man are ultimately as valid (provided they are drawn by equally sound methods) as are those drawn from Amœba, the frog or the rat; and this whether they are like or diverse from what is found in other organisms. If a student of humanity asserts that man shows certain characteristics, his assertion is not negatived by the fact that no such characteristics are to be found in other organisms. There is no *a priori* ground for sneering at the notion that man in some respects acts on principles diverse from other animals. *A priori* principles of this sort "don't go," if emergent evolution is a correct doctrine; such questions are purely matters for investigation.

Thus the biologist who is to speak authoritatively on the problems of human life must be a specialist in the biology of man, just as the authority on hookworms and liver flukes must be a specialist in helminthology. That is, he must be a student and experimenter, an actor, in the social life of man; he must be an economist, a politician, an historian, as well as a physiologist. For such an authority, if emergent evolution is a correct doctrine, the proper study of mankind is man—man taken, of course, in his setting as an organism and as part of the world; but yet an extensive and intensive study of man as a distinct emergent, a creature in his own right. Such a biologist will identify the biology, the behavior, of man with that of other organisms only critically, after detailed comparative study and demonstration of the respects in which they are identical; and he will give full weight to any evidence that they are diverse.

And if we are not to set arbitrary bounds for emergence, we may be led to admit with Ritter that a particular human individual may be an emergent; a thing set off from all others, in some respects unique; a creature that is a law unto itself, not to be compressed into any general formula. From the acceptance of this, large consequences will be found to flow.

All this will make a revolutionary change in the outlook on certain troublesome human problems. A conflict has seemed to rage between the principles of scientific method and the principles by which human beings act. Since mechanical science asserts that all action is determined by the physico-chemical conditions preceding it, in such a way that all action could be predicted from a knowledge of those conditions, it leads to fatalism, to the extinction of all stimulus to effort; of all man's attempts to guide the course of events. Ideas, ideals, purposes, beliefs—all that is mental—are left without function in the scheme of things. They ought not to exist; their existence is unaccountable.

Holding further that the future could be computed from the past, and that the laws of nature are immutable, mechanical science turns exclusively to the past for judging of the future. Nothing will be exemplified in the future that has not in principle appeared in the past. For man's affairs as for all others, the thing that hath been is the thing that shall be, and there is no new thing under the sun. The idea of altering humanity, of replacing what has been bad by what will be better, is a romantic fancy.

This doctrine is often applied specifically, with startling results. Warfare and destruction have been in the past the means of advance, through natural selection. The laws of nature are immutable; this then must continue. Rapine and murder are the means of progress. To try to stop them is to try to change the laws of nature. Gentleness, pity, humility, and the rest of the "slave virtues" are weaknesses deserving of destruction and certain to get their deserts. The only justifiable conduct is that whose powerful violence leads to triumph in the struggle for existence. Ethics does not exist in the universe of perfect evolutionary mechanism; from the latter we learn the opposite of everything by which we aspire to guide our daily lives and to organize society. Such aspirations are sickly longings to oppose the course of nature, and they are quite without influence on the course of events.

With the acceptance of the doctrine of emergent evolution, all this changes. Aspirations do influence the course of events. Thoughts, ideals, purposes, are among the determining factors for the happenings in nature. It is not strictly true that "popular approval or disapproval will not alter the course of nature," if man is a part of nature. The desires and aspirations of humanity are determiners in the operation of the universe on the same footing with physical determiners. What is to come in the future is not predictable from what has occurred in the past. The laws of nature are not immutable, in the sense that new laws shall not be exemplified as new conditions arise. Because things have occurred in a certain way in the past, it does not follow that they must thus occur in the future. This has not been the history of evolution in the past; there is no ground to expect it in the future. Scientific method is reconciled with humanism. There is nothing in legitimate science or scientific method that makes it unreasonable to hope for the appearance in the future of what has not been seen in the past. Nothing in science is incompatible with striving to realize ideals that have never yet been realized.

NOTES AND REFERENCES ON CHAPTER XVI

For general discussions of Emergent Evolution, see the following: C. Lloyd Morgan, *Emergent Evolution* (New York, 1926), and *Life, Mind and Spirit* (London, 1926); also A. O. Lovejoy, *The Discontinuities of Evolution,* in the University of California Publications in

Philosophy, Vol. 5, pp. 173–220; and W. E. Ritter, *The Unity of the Organism, or the Organismal Conception of Life* (Boston, 1919). Excellent summaries of various presentations of the doctrine of emergent evolution will be found in Wm. McDougall's *Modern Materialism and Emergent Evolution* (New York, 1929) (this volume holds that mental changes need not be accompanied by characteristic physical changes). For the relation of emergent evolution to the social, see W. M. Wheeler, *Emergent Evolution and the Development of Societies* (New York, 1928).

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